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ASSISTANT PROFESSOR OF BOTANY IN UNIVERSITY COLLEGE, LONDON.

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THE
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VOL. VI., No. 1. JANUARY 31ST, 1907.

HARRY MARSHALL WARD.

I WILLINGLY comply with the Editor's request that I would write some account of the remarkable personality of which botanical science in this country has been so untimely bereft. The story has not only an almost romantic interest of its own, but it is a not unimportant chapter in the history of our botanical school. If in telling it I am a little autobiographical, the circumstances of the case make this unavoidable.

In 1873 Professor Huxley's health compelled him to go abroad. At a very short notice I was asked to take his place at what was then the Normal School of Science at South Kensington, and give a Course of Instruction in Botany to Science Teachers, on the lines which Huxley had himself worked out for Biology generally. A lecture was given in the morning, and during the remainder of the day the students were assisted in demonstrating for themselves in the laboratory what had been taught dogmatically in the lecture-room. I secured the help of the late Professor Lawson, and it must be confessed that the task we attempted was no easy one.

At that time botanical teaching in this country was practically confined to the medical curriculum. It did not attempt to go beyond the organography of Flowering Plants and was, I take it, mainly regarded as an introduction to materia medica. While I was teaching in Dublin I had attempted to cover the whole morphology of the Vegetable Kingdom, without, however, any facilities for laboratory instruction. The South Kensington course was an opportunity for launching out more boldly. Lawson and I accordingly determined, with an audacity at which I now almost shiver, to demonstrate to our students things which for the most part we had only seen ourselves in books, and which were regarded with awe as only within the competence of the greatest masters. Our attempt was at any rate rewarded with considerable success.

The course was repeated in 1875 by Professor Vines and myself with more confidence and went on day by day for eight weeks. This was my first acquaintance with Marshall Ward, who was one of the students. He came from Manchester, where his family was well-known, and had I believe received his early training at Owens' College. He had also I think attended one of Huxley's courses, and was therefore not unfamiliar with laboratory methods. Vines and I soon discovered that we had got hold of a man of exceptional ability. In the examination at the end of the course he soared away from all the other students and stood alone at the head of the first class. The strain of the work on both teachers and students was certainly severe : there was the keenest competition amongst the best men to respond to the demands made upon them, and the tension was sometimes rather acute. On one occasion Marshall Ward fainted at his work from no other cause I think than over-excitement.

The novelty of the method attracted a good many visitors, and it was sometimes difficult, especially in the case of Kitchin Parker the comparative anatomist, to keep them from monopolising the students' microscopes. A young man, L. A. Lucas, had acquired the prescriptive right to frequent the laboratory as a previous pupil of Huxley's. Personally I had little communication with him, and he must have discovered Marshall Ward for himself, though no doubt he became aware of the opinion which Vines and I had formed.

Marshall Ward was in fact exceptionally skilful in manipulation, an excellent draughtsman, and already showed the power of seeking and grasping the principles that underlie phenomena which he so conspicuously displayed all through life. But although I was greatly interested in him, I was not in a position to suggest any career at the moment beyond taking up teaching under the Science and Art Department, for which he became officially qualified.

However the opportunity came not long after in the least expected way. He called on me one day to tell me a strange story and to ask my advice. He had received an anonymous letter telling him that if he would enter at the University of Cambridge, he would find a sufficient sum of money to his credit at Mortlock's Bank to pay his expenses. The acceptance of such a proposal involved a certain amount of risk, but I advised him to take it. By Vines's advice he became a candidate for, and secured, an open Scholarship at Christ's College and went into residence in October, 1876. On November 20th following, Lucas, who had gone to Africa, died on board the S.S. Massowah between Suakim and Jeddah at the early age of 25. He proved to have been Marshall Ward's benefactor and had made provision in his will for the continuance of the subsidy. Marshall Ward took full advantage of his opportunities and attended the teaching of Sir Michael Foster in physiology and of Professor F. M. Balfour in comparative anatomy. He took a first-class in the Natural Science Tripos in 1879. His first published paper was the result of work done in the same year in the Laboratory at Kew.

As was then customary with our young botanists Marshall Ward went to Germany for a short time and worked at Wurzburg under Sachs, whose Lectures on the Physiology of Plants he afterwards translated.

In the meantime the Coffee Industry of Ceylon was menaced by the Leaf disease, which ultimately destroyed it, and broke the Oriental Bank. Mr. (afterwards Sir Daniel) Morris, who had attended the South Kensington course in 1876, had shown that the plants could be cleansed from the *Hemileia* by dusting them with a mixture of sulphur and lime. But they speedily were re-infected. The Ceylon Government therefore asked for an expert who would devote himself to a thorough investigation of the organism which caused the disease. On the nomination of Kew, Marshall Ward was appointed in 1878. The night before he started there was a meeting of the Linnean Society. Among those present were Marshall Ward, Sir Joseph Hooker, myself, Professor Balfour, who was going to Socotra, and I think Dr. Trimen, the Director of the Royal Botanic Gardens, Peradeniya. The two last were going in the same ship with Marshall Ward. I remember that we all adjourned to the rooms of Professor Moseley at the University of London after the meeting.

Marshall Ward solved his problem as far as it could be solved. He showed that the *Hemileia* was a Uredine, and that it was disseminated by the air-borne uredospores. Had the planters, as in Southern India, preserved forest-belts between their plantations, the uredospores might have been filtered out and the disease controlled. Marshall Ward had learnt to ride before his departure, and for two years he was indefatigable in visiting on horse-back the diseased districts. But the problem, though cleared up in its scientific aspect, remained as hopeless as before. The Ceylon

Government however fully appreciated the value of Marshall Ward's work. After his return from Ceylon in 1882 he worked for a time with De Bary at Strasburg.

During his residence in Ceylon he found time thoroughly to investigate two epiphyllous organisms which were incidental to his main research. That on *Meliola* I communicated to the Royal Society and it was published in the *Philosophical Transactions.* That on an Epiphyllous Lichen I communicated to the Linnean Society. For some reason Marshall Ward was unable to be present and I had the pleasurable task of unfolding the beautiful story which he had invested with all the charm of a fairy tale. In this memoir I think he struck the key-note which ran through his work to the end. This was the quality of imagination which led him to transcend the immediate facts and guided him to a solution of a problem sometimes almost poetical in its scope and satisfying completeness. There were never any loose ends about his work, and when free-handed he generally succeeded in bringing it to a triumphant finish.

British Mycology, which had made such a splendid start with Berkeley, himself like Darwin a member of Marshall Ward's College, was practically dead. On the last serious outbreak of the potato disease in this country, the Royal Agricultural Society had invoked the aid of De Bary, though Berkeley had first described its life history. It was clear, however, that we had secured in Marshall Ward a mycologist of the first rank. The problem was how to keep him going. A chance meeting with Sir Henry Roscoe at a Dinner of the Royal Society saved the situation and secured Marshall Ward's election to a Berkeley Fellowship at Owen's College in 1882. Here he worked for three years as Assistant to Professor Williamson. In 1883 he was elected a Fellow of his old College at Cambridge, In 1885 the Regius Professorship of Botany at Glasgow became vacant by the removal of Professor Balfour to Oxford. It was hoped that the Crown would recognise Marshall Ward's colonial services by appointing him. Other influences were, however, at work, and the Government passed him over for the late Dr. MacNab. A good deal of feeling was excited, and as Professor Balfour had not actually resigned, the University refused to allow him to do so, and a dead-lock ensued, which was only solved by the Government declining to take either candidate.

This was a great disappointment to Marshall Ward, which was however in some degree mitigated by Kew obtaining for him the

Professorship of Botany in the New Forestry Department of the Royal Engineering College at Cooper's Hill. Here he remained for ten years. Its rather utilitarian atmosphere was not very congenial to him. But he had at any rate an assured position, and a laboratory to work in. He had acquired a singularly clear style in lecturing, and he knew how to "get hold" of his students, whom he used to bring to Kew every week during the summer months to study the Arboretum.

The Cooper's Hill period was fruitful in some of Marshall Ward's most brilliant work. He was never satisfied with mere morphological detail. What he always sought was the physiological purpose of which this was the mechanism. I do not doubt that he owed this, in some measure, to his Cambridge training. An admirable research on the colouring matter of Persian berries showed that it was produced by the decomposition of a glucoside by a ferment. A beautiful account of "a Lily-disease," contains the discovery that a ferment is the means by which the hyphæ penetrate the cell-walls of the host. From this time onwards, the all-importance of ferment action absorbed his attention. A curious organism had been sent me from the Eastern counties, which was used in the rustic manufacture of ginger beer. I showed it one day to Marshall Ward, and suggested his examining it. This he did in the most exhaustive way, bringing to light the important fact that its action was due to the symbiotic work of a yeast and a bacterium. This is so vigorous, under favourable circumstances, that Marshall Ward narrowly escaped a severe accident from the blowing up of his apparatus. In all these researches he showed a quality which, I think, amounts to positive genius, and which I have not myself come across, at least to the same extent, in anyone but Mr. Darwin himself. He seemed to have the gift of compelling nature to reveal its most elusive secrets. When he attacked a problem it was impossible to predict where it would land him. There was a certain subtlety in the working of his mind. He often looked at me reproachfully when I failed to visualise what he was driving at; but he could not always put it into words himself. The operations of his mind often suggested to me his own favourite ferment action.

It must, however, be confessed that this attitude had its limitations, and I think he sometimes failed to see the wood for the trees. In his investigation of the nitrogen-fixing bacteria in leguminous plants, though he added materially to our knowledge, he did not bring it to the convincing and triumphant conclusion I had hoped, and though the enormous amount of energy he devoted to the study of Bacteria led to many important discoveries, I doubt if the results were altogether adequate to the labour.

His scientific position, was however, already assured. He had by general consent put a new face on the study of Mycology in this country. In 1890 he was selected, by the Council of the Royal Society, to deliver the Croonian Lecture, and in 1893 he received the Royal Medal.

For some years Marshall Ward was engaged at the instance of the Royal Society in an investigation of the bacterial contents of Thames water. He carried it through with almost excessive conscientiousness. But I always regretted his undertaking the task. He was at his best in attacking a definite problem: he was somewhat deficient in the power of correlating masses of detail, and seeing them in their relative proportion. This, I think, shows itself in his Presidential Address to Section K of the British Association at Toronto, where long strings of authorities are quoted as if they were all of equal significance and value. He was so enthusiastic that he could not believe that everyone's work was not as good as his own.

His reports to the Royal Society on the Thames Water business were voluminous, and in the aggregate make a stout volume. But the detailed work which he also sent in for publication formed a stack of drawings and manuscript about a yard high. It was estimated that it would cost £400 to publish. It was my unfortunate duty to report upon it, and I was obliged reluctantly to arrive at the conclusion that the expenditure would not be justified. It contained, however, results of great beauty and importance, and these I persuaded Marshall Ward to publish separately from time to time. An incidental research on the bactericidal effect of light of high refrangibility has become classical. In 1895 he was appointed successor to Professor Babington at Cambridge, Mr. Francis Darwin with singular generosity waiving his own claims in Marshall Ward's favour. In the same year he was elected to the Council of the Royal Society.

Vines, Darwin, and Gardiner had laid the solid foundations of the most distinguished School of Botany in the country. Marshall Ward's successful teaching raised it to even greater importance, and the University was at last induced to provide it with adequate accomodation. It was Marshall Ward's good fortune to superintend the erection of the best equipped Botanical Institute in the country, perhaps in the world. It was mine to see my old pupil receive the King and Queen at its Inauguration. I could not but remember the difficulty I experienced when I introduced Practical Examination in Botany at Cambridge, in securing a room for the purpose.

I can hardly doubt that Marshall Ward's Cambridge work was too great a tax for even his vigorous physical powers. He added to arduous administration and teaching duties, an exhausting amount of mere bread-winning work in Lecturing, Writing, and Examining. I think he was burdened with a sense of the responsibilities of his position and the necessity of attempting to do some sort of justice to those parts of the vast field covered by his Chair with which he was least familiar. And he lacked the useful gift of "putting his work out."

But new lines of research still occupied his mind. His Ceylon work had given him an interest in the *Uredineæ*, which he never wholly dropped. Ever since wheat was cultivated in Europe, "rust" has been its scourge. The last years of Marshall Ward's life were spent in the laborious investigation of the complex problems that sprung from the relations of rust-fungi to their hosts. He satisfied himself that these cannot be accounted for by anatomical characters. What ultimate solution of the problems his fertile brain would have suggested to him is unhappily lost to us. Incidentally he finally disposed of Eriksson's mycoplasm.

The last time I heard him speak, was at the meeting of the British Association in 1904. He seemed to me to have lost something of his old fire, and, perhaps from the habit of Class-Lecturing, to labour detail more than was necessary to a scientific audience. His health began to fail after this. He seems, however, from the first to have doggedly shut his eyes to the fact. I saw him for the last time at a Meeting of the Royal Society in the following year. The hand of death was obviously upon him: he was wasted to a skeleton, and his eyes shone with an unearthly glitter. I implored him to take a long leave of absence, and a rest in a warm climate. He assured me, however, that he would soon be well. He even travelled abroad afterwards, and I believe as far as Vienna, to attend the Botanical Congress. But the end came more swiftly than I anticipated.

In this appreciation I have not attempted a systematic survey of the whole of Marshall Ward's work. But I have dwelt on enough to justify his position in the first rank of investigators. Ingenuity and dexterous skill in manipulation he had from the first. But it was my privilege to see his intellectual powers unfold and apply themselves with success to the most obscure problems. Other workers will arise, no doubt, who will attain not less distinction. But we shall have to wait a long time before we get a second Marshall Ward.

Two notes in his character only remain to be added. From first to last his soul was wrapped up in enthusiastic devotion to research. It was his whole life to a degree that I have never met with among my contemporaries. What we used laughingly to call "The Cause"—the establishment of a vigorous botanical school in this country, independent of Germany, possessed all his energies. To this must be added a noble and uncomplaining courage which enabled him to face straitened circumstances and declining health with unfailing cheerfulness.

W. T. THISELTON-DYER.

17th December, 1906.

IN response to the Editor's invitation I am attempting to give some personal impressions of Professor Marshall Ward, under whom I had the privilege of working for some years. This is a task at once both easy and difficult; everyone who knew him will realise how vivid an impression of him remains, and yet will realise as clearly how inadequate words are to convey that impression to others.

In the scientific world, Professor Ward has become eminent in virtue of his brilliant researches and organising power, but as a Professor, in his own laboratory, his great success must be traced, perhaps, more to his personal character, than to his wonderful grasp of the subject which he made his lifework.

His chief characteristic undoubtedly was his unbounded enthusiasm for work, which kept himself and his assistants always at high pressure, and his personal charm of manner was such that everyone inevitably tried to follow the example which he set.

Never shall I forget his kindly welcome when I came up to Cambridge to begin research under his supervision: at all times his attitude to his students was that of comrade and fellow-worker, rather than Professor and critic. Whilst always ready to help others, he was as ready to learn from anyone, even his most insignificant student. Even during term-time, when he was already over-busy with lectures and syndicates, he rarely allowed a day to pass without visiting each of his research students, and it was indeed remarkable how he would pass from one to another, and in a moment grasp fully the exact stage which each research had reached. His criticisms were often severe and unreserved, and his praise was very rare, but when any real success had been gained his few words of congratulation were so spontaneous and sincere, that they gave encouragement for many days to come.

Everyone understood that Professor Ward would not tolerate slackness in any form; there must be no drones in the hive, but Staff, Students and Laboratory Assistants must all alike be keen workers. As a lecturer, he was unrivalled for clearness of speech, lucid explanations and the power of awakening and rivetting interest: by vivid description, rapid drawings and the constant application of his knowledge to matters of practical importance, he kept his hearers' attention from beginning to end; and by impartial discussions of opposing theories, he cultivated in them independence of thought and a desire for further study of the subject in hand.

Whether at home or in his laboratory Professor Ward was never too busy to give advice to any who sought his help, and he was continually on the watch for opportunities when he might use his influence on behalf of those he considered worthy.

His untimely death has removed from our midst a great teacher and a true friend to those of us who knew him; but we shall never forget him nor cease to be grateful for the privilege of working with and for him. His students are now living in very many parts of the world, and through them, as well as through his public work and writings, his influence must be felt for long years to come.

M.D.

Cambridge, October, 1906.

LECTURES ON THE PHYSIOLOGY OF MOVEMENT IN PLANTS.[1]

BY FRANCIS DARWIN.

[TEXT-FIG. 1.]

III.—THE ANALYSIS OF GEOTROPISM.

THE attempt to obtain a clear insight into the nature of geotropic curvatures is comparatively modern. We owe much to the well known researches of Czapek[2] and recently we have had a no less interesting work by Fitting[3] to which I propose to call your attention to-day.

Among earlier researches in this direction may be mentioned the Power of Movement in Plants, where the attempt was, for the first time, made to distinguish between the motor and perceptive elements that go to make up geotropic and heliotropic curvatures.

The relation between excitation and reaction is one to which Fitting devotes a considerable amount of attention. An external agent,—a stimulus,—produces some sort of upset or disturbance in the protoplasm. This, which the Germans call Erregung, and we Excitation, has not necessarily any relation to movement. A slight excitation may be produced, and may die away and cease to exist, without leading to movement. We must, however, believe that even a passing excitation begins to prepare the explosion in the motor apparatus which is the result of stronger excitation. We may once more use the well worn illustration of a gun fired by hanging a weight to the trigger. A minute weight would not let off the gun, but since an accumulation of minute weights will do so, each must have its effect. Here the weights represent excitation, and the firing of the gun the motor reaction.

Let us imagine that the weight which pulls the trigger is water added drop by drop: in that case, if the previous drop has evaporated before its successor is added, the gun will never explode. We shall see that this sort of thing actually occurs in intermittent stimulation, if one unit of excitation dies out before another is added, the motor reaction does not occur. The time that an excitation takes to die out thus comes to have some importance, and has received the name Relaxation Time. The reaction, *i.e.* in this case, the geotropic curvature also finally dies out. That is to say, if we place a plant horizontal for, say ten minutes, and then rotate it on the klinostat, the act of curving continues for a certain time and then ceases.

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[1] A Course of Advanced Lectures in Botany given for the University of London at the Chelsea Physic Garden in the October term, 1906.

[2] Pringsheim's Jahrbücher, XXVII., 1895, XXXII., 1898, and elsewhere.

[3] Pringsheim's Jahrbücher, XLI., 1905.

This is a convenient place to define some other technical terms which have been found to be necessary in discussions on tropic curvature. If a plant is placed horizontal for a short time, and is then removed from gravitational stimulus by placing it on a klinostat, we may, or may not, find that geotropic curvature follows. By repeating the experiment with increasing times of exposure, we can find the minimal period of horizontality sufficient to produce a reaction. This is known as the *presentation time*,[1] and has been determined by Czapek for the radicle of the lupine as 20 minutes, by Fitting for the epicotyl of the bean as 6 or 7 minutes. It is important not to confuse the presentation time with another factor in the problem. It is a natural mistake to suppose because the plant requires say six minutes' exposure to produce a curvature, that this period is necessary for the act of perception. But this is wrong; it is quite conceivable that the plant perceives the stimulus within a few seconds of being horizontal, but that such a small excitation is produced that no reaction follows. We must in fact distinguish between the presentation time, and the excitation time, *i.e.*, the period necessary for the perception of the stimulus. If every brief period during which a plant is not vertical were to produce a reaction it would be stimulated to a geotropic curvature by every breath of wind which bends its stem, and it would be constantly bending uselessly as Fitting points out. Fitting has, as a matter of fact, shown by experiment that plants are stimulated by a few seconds' horizontality, so that it seems likely that the existence of presentation time is an adaptation by which the plant avoids useless bendings. The plant may be imagined as so attuned to circumstance, that it cannot curve unless the loss of verticality has lasted so long that it seems likely to be permanent, and therefore gives a situation which must be dealt with. One other term which we owe to Czapek must also be referred to, *viz.*, the *reaction time*, *i.e.*, the period of permanent horizontality required to produce a curvature. For a Lupine radicle the reaction time is about an hour. When we begin to study a stimulus, we naturally inquire how the reaction is affected by altering the intensity of stimulation. Czapek worked with a centrifugal machine, employing varying rates of rotation and various radii. There is, however, another method of diminishing the stimulus of gravity, namely by placing the organ obliquely. If we believe, according to the statolith theory, that the gravitational stimulus depends on the pressure of heavy particles on the protoplasm of the longitudinal cell walls, it is clear that the pressure is nil when the organ is vertical, and greatest when it is horizontal, and for intermediate oblique positions the pressure will vary with the size of the angle which the organ makes with the vertical. Sachs deduced this law of the stimulus being proportional to the sine, chiefly from theoretic considerations, and Fitting has proved it to be approximately true. This, which is generally known as the problem of the position of maximum stimulation, has led to a mass of contradictory experiment.

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[1] Czapek.

In 1888 Miss Bateson and I[1] made some attempt to solve it. Shoots were fixed (by being pinned to boards) in three positions, *viz.*, horizontal, 60° apex upwards, and apex downwards at the same angle. They were left so for two hours, when they were released and placed in water for an hour. The angles through which they curved were then recorded; the following figures give the averages in round numbers:—

	Curvature.	Or as
Horizontal ...	58° ...	100
60° above Hor.	43 ...	73
60° below Hor.	43 ...	73

There was great variability in the individual plants, but the average shows a distinct difference in favour of the horizontal position.

The next experiments were those of Czapek.[2] He fixed plant-organs at various angles to the vertical so that they could not curve. After some time they were released and placed in the klinostat for twenty-four hours, when the curvatures were measured. The general result is that the maximum curvature was produced by exposure at 135° from the normal. This means that the maximum position for apogeotropism is 45° below the horizontal, and *vice versâ* for pros-geotropic organs.

In the light of recent work there can be no doubt that neither our experiments of 1888 or Czapek's are really adapted to solve the question. It is quite conceivable that in a given time a weak stimulus might be able to produce as much curvature as a stronger one. Just as a small weight and a bigger weight may both be able to fire a gun, and thus produce equal effects though they themselves are not equal.

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[1] Annals of Botany, Vol. II., p. 65.

[2] Pringsheim's Jahrb., XXVII., 1895, p. 287.

The method used by Miss Pertz[1] is a much better one, namely that of the intermittent klinostat, by means of which apogeotropic plants were alternately placed at 45° above and below the horizon. The nature of the resulting curvature seemed to show that Czapek is right and that —45° is more effective than +45°. But this result must not be trusted owing to an error to which I shall return. Other experiments of the same kind were made by Newcombe[2] and by Miss Haynes[3] who alternated various angular positions and concluded that the horizontal is that of maximum stimulation. Fitting has undoubtedly solved the question by a new method of using the klinostat, namely by making the axis oblique instead of horizontal. Its novelty is not at first apparent, for if the organ is parallel to the axis, the oblique klinostat does not differ from the horizontal one. The gravitation stimulus will be less than with the horizontal klinostat, but it will be evenly distributed about the plant just as with the ordinary instrument. But if the plant is not parallel to the axis, the result will be different, as will be seen in the accompanying diagram.

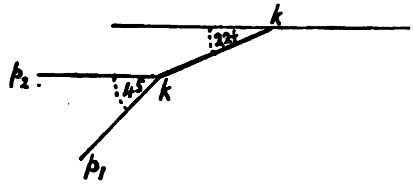

Figure illustrating the oblique klinostat.

If, for example, the axis, kk, of the klinostat is 22½° below the horizon, and the plant, p, makes an angle of 22½° with kk, then, assuming it to be an intermittent klinostat (which rotates through 180° at regular intervals of time), the alternating positions of the plant will be p_1 and p_2, *i.e.*, horizontal and —45°. If p_1 is the position of maximum stimulation, the plant will tend to curve inwards towards the axis of rotation. This is obvious since, on the hypothesis, the tendency to bend upwards in position p_1 is stronger than the corresponding tendency in position p_2. In the same way if the horizontal is the position of maximum stimulation the resultant curve will be away from the axis. This is what Fitting found, all his experiments were in favour of the excitation being greater at 0° (horizontal) than at —45°. The experiment resembles a "tug-of war" between opposing stimuli: the proof that one side is stronger than the other, is that they haul their opponents over the mark; so in the case of the plants a slight curve in one direction tells us which of the opposing excitations is the stronger.

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[1] Annals Bot. XIII., 1899, p. 620. Czapek had previously used the method for diageotropic roots, see Sitz K. Akad. Wien 104, 1895.

[2] Annals of Botany, 1905.

[3] American Naturalist, 1905.

The fact that the horizontal is actually the position of maximum stimulation can only be proved by repeating the experiment with alternating positions of 0° (horizontal) and 22½°, then with 0° and 11°, and so on. Fitting has combined 0 and 22½, proving that the position of maximum excitation is not more than 11° from the horizontal.

Fitting made a very interesting modification of his method by using the intermittent klinostat with unequal times. Thus the positions 0° and —45°, with equal exposures in the alternating positions, cause curvature, but if the plant is kept for fourteen minutes in the position of weak stimulation (—45°) and ten minutes in that of stronger stimulation (0°) and so on alternately, it does not curve, but remains straight. Now 14 : 10 = 1 : 0·71, that is in the proportion of sin 90 : sin 45. If to nullify the effect of alternate exposure in the positions —45° and horizontal, we have to make the periods of exposure as sin 90 : sin 45, it is clear that the excitations are as sin 45 : sin 90, that is in the proportion of the sines of the angles which the plant makes with the vertical. The same relation was obtained by alternating other positions, as shown in the following table:—

	Angle with vertical.		
Alternate positions ...	60° and 90° ...	30° and 90° ...	15° and 90°
Times of exposure ...	1 : 0·87 ...	1 : 0·5 ...	1 : 0·26
Sines	0·87 : 1 ...	0·5 : 1 ...	0·2 : 1

It is thus proved that the excitation is directly proportional to the time of exposure and to the sine of the angle made by the plant with the vertical. These experiments, which have been described as made with the intermittent klinostat, give a similar result with the continuous instrument. This is a very interesting method of proving that the stimulus of gravity is continuously perceived by plants rotating on the klinostat.

Upon this fact depends Fitting's method of determining the *perception* or *excitation* time. Most observers have employed a continuous klinostat rotating in about 20′, but Fitting finds the result to be the same with rotations of 12″, 6″ and even 1″. Take the case of an oblique klinostat rotating in 2″, here the plant will be for not more than 1″ in each of the alternate positions of unequal stimulation. And since under these conditions a curvature is the result, it is certain that exposure of 1″ produces excitation.[1] The same result followed with rotation of 1″; there can be little doubt therefore that excitation is practically instantaneous.

By the same method it was strikingly shown that *perception* time and *reaction* time have nothing to do with each other. Thus grass haulms when left horizontal do not curve for many hours, yet when placed on an oblique klinostat rotating once in 6″ they give a geotropic result, shewing a perception time of not more than 3″.

Some very interesting results were obtained by combining angles which are nearer together than 0° and 45°. Thus +3° and —9°, differing by 6°, produced no curvature; but with larger angles differing also by 6° a result did follow, thus +55° and —61° gave a curvature. Even with +86° and —88° a result was obtained. In this case the axis of the klinostat was only 1° from the horizontal. This suggests that when Miss Pertz believed herself to be experimenting with a horizontal klinostat she was accidentally using an oblique one, and that the curvatures she obtained when the plants were supposed to be +45° and 45°, really occurred with plants at say 44° and 46°. [2]

Carelessly considered, it would seem that in Fitting's experiments the plant is more sensitive when it is nearly vertical than when it is horizontal, *i.e.*, that it is less sensitive when it is in the optimum position. But probably it is a case of the Weber-Fechner law. Our eyes distinguish between two sources of light when they differ by 1%. So that if the light is very faint, 1% is a very minute absolute difference, whereas with a bright light 1% is a big amount. This is probably true, *mutatis mutandis*, of Fitting's results.

Another subject of investigation was the plant's power of distinguishing between exposures of different duration. For this purpose the intermittent klinostat was arranged so that the plant remained for unequal periods in the alternate positions. When the difference of the periods had approximately reached its limit the resulting curvature was very small, and required three to four hours for its completion. This was effected by the plant being alternately horizontal for 353″ and, after a sudden rotation through 180°, horizontal in the other position for 367″. Thus the plant curves when the alternating periods of exposure differ by 4%, and this percentage was found to hold for all observable rates of rotation. Thus if the plant is alternately exposed for 25″ and 26″ a slight curvature results, and here again the exposures are as 100 : 104.

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[1] With these rapid rotations an effective amount of centrifugal force is produced, but this was discounted by the arrangement of the experiment.

[2] In the Annals of Botany, XIX, p. 569, Miss Pertz shows that with a carefully levelled klinostat the results confirm those of Fitting.

Other very interesting results are obtained by intermittent stimulation, namely a knowledge of the *relaxation* time, *i.e.*, the time required for the practical extinction of the state of excitation. The methods were two, *i.e.* (i.) to expose the plant alternately in the horizontal and vertical positions : (ii.) periods of horizontality were alternated with periods of continuous rotation. Both methods give alternations of excitation and repose, and the two methods are mutually confirmatory. When the period of Rest is to the period of Stimulation as 5 : 1, the reaction occurs as quickly as when the plant is exposed to continuous stimulation. When Rest is to Stimulus as 11 : 1, slight variable curves occur after three to five hours. When Rest is to Stimulus as 16 : 1, no curvature follows. These results were obtained with epicotyls of *Vicia faba* : with roots of *V. faba* there was no curve with 5 : 1, and hardly any, with 3 : 1. The results were found to depend strictly on the *proportion* between the times of stimulation and repose, and this proportion was the same whether the actual periods of exposure were short or long. It is clear that the above experiments give the relaxation time. When the period of Rest was to that of Stimulation as 16 : 1, no reaction followed because the excitation of the first stimulus had died out before the second occurred, and the second before the third, so that there was no possibility of adding together the excitations.

Let us return to intermittent stimulation, when the proportion between Rest and Stimulus is such that the excitation from one stimulus does *not* die out before the next is added. Fitting tried the following experiment. A plant A is exposed to intermittent stimulation, *i.e.*, to alternate periods of repose and excitation. At the same time a similar plant B is exposed to continuous stimulation. Then both A and B are placed on the continuous klinostat so as to be freed from further geotropic action. This is in fact the method for determining the presentation time, *i.e.*, the period of excitation needed to produce by after-effect a distinct curve.

It was found that plant A had a much longer presentation time than B, that is to say the intermittent stimulation had to be kept going for a time longer than the exposure to continuous stimulus. But when the individual periods during which A had been stimulated were added together their sum was found to equal the presentation time of B. Thus if the presentation time of B was twenty minutes, then A would have to remain for forty minutes on an intermittent klinostat which gave equal intervals of rest and stimulation. Only one half of the forty minutes is made up of actual stimulation, so that the presentation time is really twenty minutes. It may also be made up of two exposures of ten minutes each by using a klinostat rotating once in 20°, or of twenty exposures of 1° each with a klinostat rotating in two minutes.

The fact that, in the case of geotropism, intermittent stimulation is a simple case of addition, has interesting bearings. If a series of short exposures is equal to the effect of a single long exposure, it is certain that each of the short exposures must have set going part of the motor machinery,—a conclusion which has already been referred to, but without the experimental evidence here given.

Fitting gives an interesting discussion on the relation between the times of reaction and relaxation. This is a point well worthy of attention, but it is one on which want of time forbids our entering.

CURRENT INVESTIGATIONS IN ECONOMIC BOTANY

(*Continued from Vol. V., p. 86*),

By William G. Freeman.

The Sugar Beet.

The sugar beet is a cultivated variety of *Beta maritima*. The wild, comparatively slender-rooted form of the species is well-known in this country as a maritime plant, occurring on sea shores, in clefts and on ledges on sea cliffs and similar situations. It ranges through the Mediterranean region, the shore of the Caspian, Persia, and the Canary Islands. The plant was known to cultivation before the Christian Era, and the ancients were familiar with red and white-fleshed varieties.

From the original type, the wild *Beta maritima*, there have been obtained by selection, three distinct cultivated races, the garden beet, the mangold wurzel, and the sugar beet. The characteristics of the two former are familiar to everyone, they are grown respectively as a vegetable, and as food for cattle. The sugar beet is white fleshed, not red as the ordinary beet, and is more fibrous and roots deeper in the soil than the mangold wurzel. Selection along different lines has produced very wide divergence in the sugar contents of the two last named plants, and whilst the mangold wurzel contains more or less about 8 per cent. of sugars, the sugar beet contains as much as 18 per cent. of these same bodies. Our immediate interest however is centred in the sugar beet, the cultivation of which is so important as to place Europe first amongst the continents as regards sugar-production, a position attained during the past century and affording perhaps the most striking example of the successful application of science to industry in the plant world.

Historical.

In 1580 Olivier des Serres recorded that the red beet had not long been introduced into Europe and that "the juice yielded on boiling is similar to sugar sirup." No practical result followed this and attention was not directed to the beet as a possible commercial source of sugar until 1747 when Marggraf who had investigated a large number of plants to ascertain their sugar contents, published his "*Experiences Chymiques faites dans le dessein de tirer un veritable sucre de diverses plantes qui croissent dans nos countrees.*" He sliced and dried the plants, ground them to powder and exhausted with dilute alcohol and crystallized out the sugars. His methods were only suited to the laboratory, but he urged the importance of the beet as the source of a possible sugar industry.

Another long interval, this time half a century, elapsed and it was not until 1797 that Achard, a French refugee and a former pupil of Marggraf again took up the work. After much investigation he was successful in extracting sugar from the beet on a considerable scale, and in 1799 he presented a specimen of the sugar and gave a description of his method to the Institute of France. In this paper he stated that the cost of production should not exceed about 3d. per lb. Considerable doubt and ridicule was cast upon his work, but even this was fruitful, as interest was aroused and a commission of chemists was appointed to inquire into the question and to repeat Achard's experiments.

The report of the commission of enquiry was presented in 1800. Investigations on other plants are summarized, and attention drawn to the failure which had attended the efforts to introduce the sugar-cane and the sugar-maple into France. In the beet itself they found a little over 6 per cent of sugar. By repeating Marggraf's experiments a muscovado sugar, of a dark colour and disagreeable taste was obtained, at an estimated expense of 9d. per lb. Among the conclusions arrived at, the commission states "That admitting the results of the experiments it remains to be demonstrated that the beet may, up to a certain point, supplant the sugar-cane."

The next important step appears to have been taken in Germany, where in 1805 Baron de Koppy built a factory in Lower Silesia capable of dealing with abont 500 tons of roots in a year. Achard also founded a factory of his own.

The production of sugar from the beet, and its competition with the sugar-cane was not however allowed to remain a question of purely scientific and commercial interest. Sugar production early became involved in politics, a position from which it has not yet finally escaped. At the time now under discussion, approximately a century ago, political considerations played a very important part. Napoleon I. issued the decrees of Berlin and Milan, establishing a Continental blockade, designed to exclude British products and manufactures and particularly the products of the British Colonies, the more important then being sugar, indigo and cotton. The already established beet sugar factories made increased profits, active investigations were carried out in France to find substitutes for British colonial produce, and incidentally the French wine trade suffered. As an instance of the efforts made to produce sugar locally it may be noted that the manufacture of this article from grapes was encouraged by money grants. Further research was made in beet sugar production and in 1811 the Emperor decreed that some 79,000 acres should be placed under sugar beet cultivation in the Empire. So long as Napoleon was able to encourage the industry all went well, but with his fall it fell also, one factory only surviving. Yet the practicability of sugar production in Europe had been demonstrated, factories soon sprang up again, and in 1829 the crop was returned as 4,000 tons of sugar. The German industry collapsed also with Napoleon's fall and did not revive until about 1835. Its modern development in Europe is dealt with later.

In the United States attention was first turned to the sugar beet in 1830, when some experiments were made without however leading to any permanent result. A second, entirely fresh beginning was made in 1863, and this has resulted in the present, comparatively small, but increasing beet sugar industry of that country.

In many other countries of the temperate regions, including Great Britain and Ireland, efforts have been, and are being, made to cultivate the plant for sugar production. In no case however as yet have they lead to any permanent commercial results.

IMPROVEMENT OF THE SUGAR BEET.

As in the case of the sugar-cane increase in sugar contents, combined with a high ratio of "purity" is one of the principal objects to be attained in "improving" the plant from the point of view of the sugar producer. The great practical difficulties to be surmounted in improving the sugar-cane have already been dwelt upon (Vol. V. pp. 86-7). They are partly due to the large size of the plant, the long periods which must elapse between obtaining seed and a crop on a commercial scale, the expense, and many other factors, *e.g.* that the full value of the megass or crushed cane, to mention only one, are of the highest importance under the conditions of sugar cane cultivation and may even cause the rejection by the planter of a variety of cane exceptionally rich in sugar.

The beet offers a much simpler problem. The plants are small, occupy but little room, and are consequently easier to work with and much less costly. The waste material does not play so important a part because in temperate climates fuel is usually cheaper and more abundant than in the tropics.

More important still is the biennial character of the plant, which allows roots to be selected at the end of their first year, and seed to be obtained from the same individuals in the second year for the third year's crop. This will, perhaps, be better appreciated if we sketch roughly the mode of cultivation and selection practised.

Beet "balls" each containing several seeds are sown, and the resulting seedlings thinned out. They grow during the summer, and the crop is dug before the approach of frost. The leafy "tops" are cut off, and the roots used at once for sugar manufacture, or stored (1) for extraction of sugar in the spring or (2) for seed purposes.

In the latter case, roots are selected according to (1) weight, those of about 20 to 24 oz. being preferred, (2) shape—the best, being regular and smooth, and (3) general appearance. The selected roots are kept in a silo. In the following spring they are gone over, and a further selection made for (4) keeping qualities, those which have not proved good keepers being rejected. The final selections for (5) sugar contents and (6) co-efficient of purity are now made.

The old method was to take the specific gravity of the whole root. Each was cleaned externally and immersed in brine of a definite strength. The heavy or "good" roots sank, whilst the light roots floated and were rejected. This method was crude, not very reliable, and moreover gave no clue to the important co-efficient of purity.

A better method is to remove, with proper precautions, a small cylindrical piece, weighing about half an ounce, of the root. The juice from this piece is expressed, its specific gravity accurately determined, and its sucrose contents estimated by a polariscope reading. From the figures so obtained, the percentage of sugar present, and the co-efficient of purity are known. In one particular experiment out of 5,091 roots selected for external characters and afterwards tested for sugar contents, 57 had more than 18 per cent. of sucrose, 1,758 between 15 and 18 per cent., and 3,276 between 12 and 15 per cent. The roots so tested are not injured. They can be planted in the spring of the second year, and will bear a crop of seed in the autumn of the same year.

The name of Vilmorin is always associated with the improvement of the sugar beet, and as an example of his results achieved by careful selection, we may instance those recorded in the

Comptes Rendus for 1856. Within the period of three generations only, the selected roots yielded juice of a mean specific gravity of 1·075, and a maximum of 1·087. These figures correspond to sugar contents of 16 and 21 per cent, whereas in the stock plants the mean specific gravity was 1·042 and the maximum 1·066, indicative of a range of sugar contents from 8 to 12 per cent only.

In Germany the greatest importance is attached to proper seed selection, because it is realized by practical men that on this the percentage of sugar obtained from the resulting crop largely depends. The system of organization adopted by the large factories allows them to control and supervise the work, and to ensure having their crops grown only from seed chosen, with every care, in respect to their own particular requirements. The roots too when purchased by the factories are valued according to a sliding scale based on their sucrose contents.

Increase in sugar contents results in a great saving of labour and in other ways reduces cost of production. Thus in 1880-81 to make one ton of sugar in Germany required 11·37 tons of roots. By 1899-1900 the percentage of sugar had been so augmented that 7·37 tons of roots yielded the same quantity of sugar, a reduction of about 40 per cent. in the weight of material to be dug, topped, transported, washed, sliced, extracted, and dealt with in other ways.

Although the sugar beet has proved itself more adapted to rapid improvement than the sugar-cane, the preparation of good sugar from the beet was not so easy as in the case of its commercial rival. These difficulties have, however, been overcome, and the net result of the joint work of botanist, chemist, and engineer has been that Europe, from being the least important of the continents as regards sugar production, now occupies the foremost place. Europe now produces more of the sugar which enters the commercial market of the world than all the rest of the world put together.

INFLUENCE OF ENVIRONMENT.

In the United States of America efforts have been directed by the Department of Agriculture, to determining the influence of the environment upon the composition of the sugar beet. This work has been carried out by the Bureaus of Chemistry, Meteorology, and Botany, and the Experiment Stations in the various States, and is a good example of the co-operation which the organization of the United States Department of Agriculture renders possible, These results are very interesting, but as might be expected when experiments are conducted in distant localities the problem is not easy to solve, as many factors have to be taken into consideration.

The plotted results show, however, that there is a close agreement between latitude and sugar contents. In high latitudes the beets contain a high percentage of sugar and *vice versâ.* As might be deduced from this variation with latitude, the sugar content decreases with increase of temperature. Another point, of considerable physiological interest, is that full sunlight and diffused light are apparently equally effective for sugar production, but that low sugar content is generally associated with short days, and high sugar content with long days. As also is known for some other plants, the actual quantity of rain which falls during a year has less influence on the plant than the manner in which it is distributed through the year.

THE ASSOCIATION OF ECONOMIC BIOLOGISTS.

CAMBRIDGE MEETING, JANUARY, 1907.

THIS Association was founded in 1904 to promote and advance the science of Economic Biology in its agricultural, horticultural, medical and commercial aspects, the inaugural meeting being held in the apartments of the Linnean Society, London. Birmingham (the home of the Association), Liverpool, and lastly Cambridge have been the scenes of the subsequent gatherings. The Cambridge meeting was held on January 9th, 10th and 11th, 1907, in the Lecture Theatre of the Pathological Department of the University, and the members were greatly indebted to the Medical Staff and to the authorities of Christ's College for the kind arrangements made for their reception.

Mr. A. E. Shipley, F.R.S. took "Sea Fisheries" as the theme of his Presidential address, and of the other fourteen papers presented during the meeting, rather more than half were zoological, although several were of interest also to the Botanist, inasmuch as they dealt with various plant pests such as the black currant gall-mite, grain weevils and a scale disease of the olive.

Mr. R. H. Biffen gave a summary of some of the interesting and important results of the work on cereal breeding conducted by the Agricultural Department of the University. The paper was valuable not only for its economic interest, but also for the remarkably clear exposition given of Mendelian laws.

Mr. E. S. Salmon dealt with the American Gooseberry Mildew, bringing forward a mass of evidence to demonstrate that it was an introduced, epidemic, fungus disease invading Europe, and advocating legislative action for its suppression. The paper lead to an interesting discussion, in the course of which Professor Middleton stated the position of the Board of Agriculture.

The Spruce-gall and Larch-blight diseases caused by *Chermes* were described by Mr. E. R. Burdon, who traced in detail the morphological and anatomical changes induced in the plants attacked, as well as the complicated life-history of the aggressor.

Mr. W. G. Freeman's paper on the Geographical Distribution, natural and artificial, of the principal rubber-yielding plants, summarized the present position of rubber-production and pointed out the complexity of the factors controlling the introduction and cultivation of these plants in new countries. In a second paper Mr. Freeman illustrated the use of economic botanical collections in the teaching of geography.

A full account of the meeting and the papers read will appear in due course in the proceedings of the Association. It is proposed to hold the next meeting in London, perhaps at the Imperial Institute, South Kensington, in July, and the succeeding meeting in Edinburgh at Easter, 1908. It is gratifying to be able to record that the Association continues to gain strength in a satisfactory manner, nearly thirty new members being elected at Cambridge. In common with many other gatherings the value of the Association is not to be gauged merely by the papers and discussions. Problems in Economic Biology are frequently very intricate. The co-operation of Botanist and Zoologist is often advisable, and sometimes essential. Meetings such as these, in which workers in various branches of applied Biology gather together, under pleasant social conditions, with opportunities for informal discussion of topics of mutual interest, will undoubtedly play an increasingly useful part.

W.G.F.

* * *

R. Madley, Printer, 151, Whitfield Street, Fitzroy Square, W.

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THE

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EDITED BY A. G. TANSLEY, M.A., F.L.S.

ASSISTANT PROFESSOR OF BOTANY IN UNIVERSITY COLLEGE, LONDON.

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LECTURES ON THE PHYSIOLOGY OF MOVEMENT IN PLANTS. V.—THE SENSE ORGANS FOR GRAVITY AND LIGHT - - - - - - - - - - *Francis Darwin.*

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NEW PHYTOLOGIST.

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LECTURES ON THE EVOLUTION OF THE FILICINEAN VASCULAR SYSTEM.[1]

BY A. G. TANSLEY

(Lecturer on Plant Anatomy at University College, London).

[TEXT-FIGS. 1—22].

II.—THE BOTRYOPTERIDEÆ.

THE Palæozoic forms grouped under the family name Botryopterideæ are in many respects the most primitive ferns known. Their sporangia are intermediate between the eusporangiate and the leptosporangiate types, having a considerable resemblance to those of the Osmundaceæ. Their vascular structure shows a very considerable range, but the various types have a good deal in common and present suggestive resemblances to some of the primitive Cycadofilices, as well as to the Osmundaceæ and Hymenophyllaceæ among recent ferns. Arber is of opinion[2] that the Botryopterideæ (or rather the larger ill-defined group of "Primofilices" in which he includes the Botryopterideæ) had passed the maximum phase of their development in later Palæozoic times when the Cycadofilices were a dominant group, while the modern Leptosporangiate Ferns had scarcely emerged as a definite phylum. All these considerations point to the probability that the Botryopterideæ stand near the ancestors of the different phyla of fern-like plants.

In general characters[3] these plants were certainly true ferns in the modern sense. In habit they appear to have varied in much the same way as the members of a modern leptosporangiate family frequently do, some having comparatively short rhizomes with closely crowded leaves, others having longer internodes and creeping or climbing stems. Of the leaves themselves we do not know a great deal. Certain impressions known as *Schizopteris* and *Schizostachys*, the former a large fleshy bipinnate frond, are probably the sterile and fertile leaves of *Zygopteris*, and Renault figures the flabellate leaflet or pinna of a frond of *Botryopteris.* The fronds were apparently often dimorphic, and the sporangia were sometimes, at least, borne terminally on ultimate branchlets of a frond with reduced lamina. These sporangial pedicels were often crowded and show signs of dichotomous branching. In *Stauropteris oldhamia* (a frond whose stem is unknown but which shows strong affinity to, though its sporangia do not exactly conform with those of Botryopterideæ) the ultimate branchlets were in crowded tufts with terminal sporangia. Some species of *Zygopteris* have axillary branching, and the relation of the stele of the branch to that of the leaf-trace is exactly the same as in the Hymenophyllaceæ.

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[1] A Course of Advanced Lectures in Botany given for the University of London at University College in the Lent Term, 1907.

[2] Arber, '06. [3] Scott, '00.

The general structure of the vascular system of the Botryopterideæ shows, as we have said, very considerable variety. The Schizæaceæ, among modern ferns, have a great range of vascular structure, both in stem and petiole, but they are far surpassed by the Botryopterideæ, the variety of whose petiolar structure is in fact one of their most striking peculiarities, quite unparalleled in modern ferns. The stem-structure, though by no means uniform, has points of resemblance throughout the family.

The simplest type of stele is a solid cylindrical strand of pitted scalariform tracheids containing no parenchyma and surrounded by phloem. This is found in the genera *Grammatopteris* and *Tubicaulis.* It is probably the real "protostele," *i.e.*, the most primitive type of vascular strand found in the axis of vascular plants. Spiral protoxylem has not been detected in these types, but, judging from other members of the family and from the analogy of modern ferns, that is probably because growth in length was not rapid. Some elements are narrower than others, but there is no particular evidence that these represent protoxylem.

The mixture of transversely elongated and more or less isodiametric pits (Fig. 1) in many of these forms is of interest. Miss Stopes[1] has suggested that the possession of circular pits, a character shared by the Cycadofilices, some Ophioglossaceæ and Gymnosperms, is a sign that the Botryopterideæ are a step in advance of the typical ferns, which possess only scalariform tracheids. It is significant however that both long and short types of pit are found in the simple water-conducting elements of the Pallavicinia-group of Liverworts, and it is not difficult to see how these mixed types could give rise to both the scalariform and the "pitted" type of tracheid. It must also be remembered that both types of pitting are sometimes found in one and the same tracheid among the Angiosperms, so that we must be somewhat cautious in attaching phylogenetic significance to this character.

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[1] Stopes, '06.

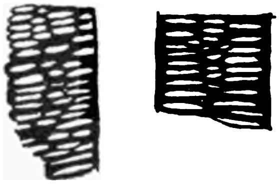

Fig. 1. Portions of two tracheids of "*Rachiopteris cylindrica*" showing intermediate forms between the "scalariform" and "pitted" conditions. Univ. Coll. Collection, K 15. × 450.

In both genera the stem was upright and the organisation radial, the phyllotaxy being a fairly high spiral. The leaf-traces leave the stele as simple band-shaped strands, which in *Grammatopteris* (Fig. 2) remain simple tangentially orientated bands in the petiole, according to Renault's figures, while in *Tubicaulis* (Fig. 3) they become C-shaped in cross section, but with the concavity of the C turned *outwards*, directly the reverse of the orientation typical of the modern ferns. We shall have to return to this peculiar orientation presently.

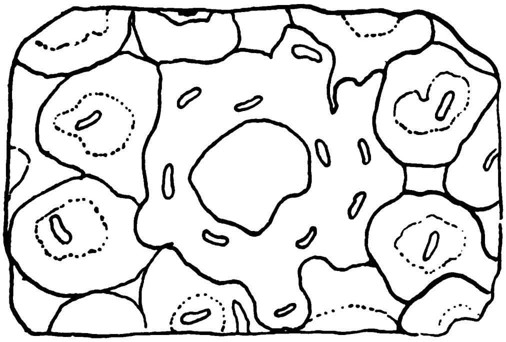

Fig. 2. *Grammatopteris Rigolotti*. T.S. of stem showing solid stele, band-shaped leaf-traces, and the bases of petioles with band-shaped vascular strands. After Renault.

We know practically nothing in either case of the type of frond or of the branching of the petiolar strand—information which would be of great interest—but assuming that the leaf-trace of *Grammatopteris* is correctly described, we may perhaps fairly regard it as a very slight departure from our hypothetical primitive type. The tangential extension of the leaf-trace may be regarded as a direct consequence of the branching of the frond in that plane, such as we find for instance in the bases of the flabellate laminæ of the erect species of *Pallavicinia* and allied genera, while the great increase in diameter of the stele of the stem is a response to the crowding of leaf-traces and the consequent necessity for the supply of a great number in a short distance.

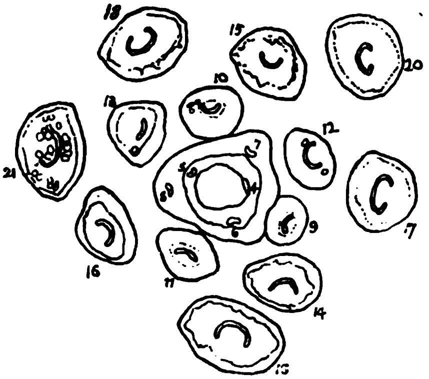

Fig. 3. *Tubicaulis Solenites.* Showing a type of organisation like that of *Grammatopteris* but with C-shaped petiolar vascular strands, the concavity of the C facing away from the stem axis. After Stenzel.

The vascular cylinder of the stem of *Botryopteris* likewise has solid xylem, but this contains fairly constantly a central strand of small tracheids (Fig. 4) which very likely represent protoxylem,

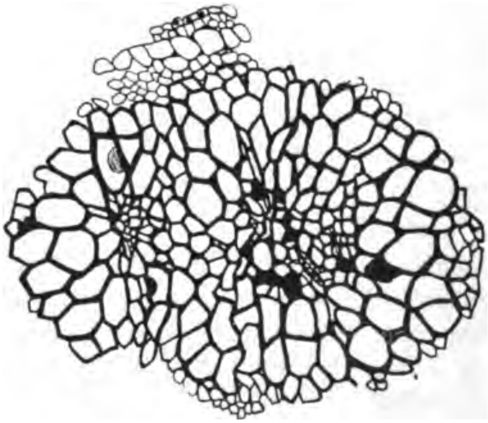

Fig. 4. "*Rachiopteris cylindrica.*" The solid xylem of the stele is preparing to branch, and a second group of small tracheids is seen on the left. The branch of the stele may be destined for a stem branch or for a leaf-trace. The tissue surrounding the xylem has been put in at the top of the figure only; the large thin-walled elements are probably sieve-tubes. Univ. Coll. Collection, K 14, × 50.

though we do not yet know if it contains spiral elements. The leaves are not very closely set and the diameter of the leaf-trace is not much less than that of the stele. The smallest elements of the leaf-trace are situated on its adaxial border and are probably continuous with those in the centre of the stele, though they may apparently run down for some little distance below the insertion of the trace before fusion occurs.[1] Here we have an *endarch*[2] structure of the stele and leaf-trace. The protoxylem of the trace may be seen to segregate into three groups and these become the points of the ω-shaped petiolar strand characteristic of the genus (Fig. 5.) The branching of this strand is somewhat obscure, and we cannot at present pretend to explain the origin or significance of its peculiar form, though it is likely that its relation to the branching of the frond will turn out to be of the same general character as that obtaining in *Zygopteris*, which we must presently discuss.

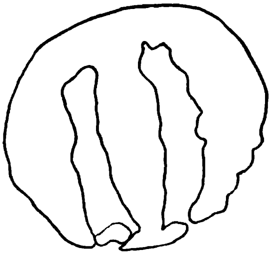

Fig. 5. *Botryopteris forensis*. From Grand 'Croix. Outline of xylem of petiolar strand. Univ. Coll. Collection, K 4. × 13.

There are grounds for believing that the endarchy of the Botryopteridean stele is a primitive character. A comparative consideration of the evolution of the multicellular axis among Algæ and Bryophytes leads to the conclusion that there is a fundamental tendency to develop elongated, relatively passive, tissue in the centre of the axis. This tissue is used for conduction where the construction of the plant requires it, and thus the primitive "protostele" originates. If this strand is sufficiently bulky and its elements do not develop simultaneously, the tendency for the more central elements to mature first will still hold, and thus, when there is differentiation between proto- and meta-xylem, give rise to endarch structure. A further expression of the same tendency is to be found in the early maturation of the pith in the medullated stems of vascular plants generally. According to our basal hypothesis the primitive assimilating frond should also possess central protoxylem in its vascular strand. Apparently we do not get this hypothetically primitive condition realised in the Botryopterideæ, which certainly possessed elaborate and highly evolved fronds. We shall see in the next lecture that the central protoxylem of the petiolar strand in certain Hymenophyllaceæ may possibly be interpreted in this way. There is no doubt, however, that if endarchy is primitive in the protostelic and immediately derived types, it very rapidly gives place to mesarchy and exarchy in response to various demands, and it is not difficult to show how this may have occurred. On the other hand it is ~~it~~ very difficult to conceive of exarchy as original and endarchy as derived in such forms as the Botryopterideæ, and this consideration must be allowed due weight in formulating our general theory.

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[1] Our information on these points is not at present at all full. Dr. Scott is, however, understood to be now working at the Botryopterideæ, and no doubt he will soon clear up many doubtful points in their anatomy.

[2] The term "endarch" applied to a leaf-trace means that the protoxylem is situated on the adaxial border of the xylem-strand, which is conceived of as representing *part* of the stele of the stem.

In *Zygopteris* (Fig. 6) we have a more elaborate type of stele.

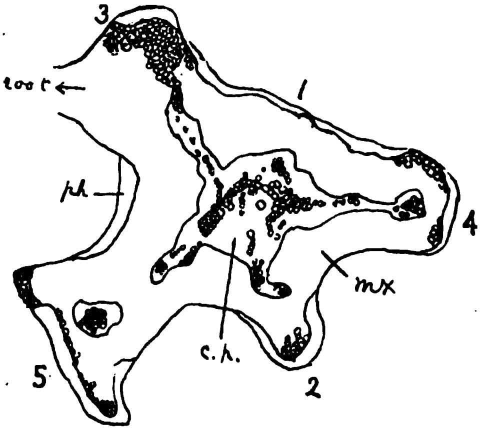

Fig. 6. *Zygopteris Grayi*. Diagram of the stele of the stem. *c.p.*, central parenchyma, with numerous narrow tracheids, which are indicated. *mx.*, metaxylem: the narrow peripheral tracheids are also indicated. On the outer edge of the xylem thin-walled tissue remains in places: this represents phloem (*ph.*) and pericyclic tissue. The numbers refer to leaf-traces. After Scott.

It has a lobed instead of a circular outline, and the ends of the lobes are successively detached as leaf-traces. The centre of the stele no longer consists of a solid mass of tracheids, but is filled with delicate parenchyma intermingled with narrow tracheids forming a connected system which extends into the arms of th stele and parts of which become included in the leaf-traces (Figs. 6 and 7).

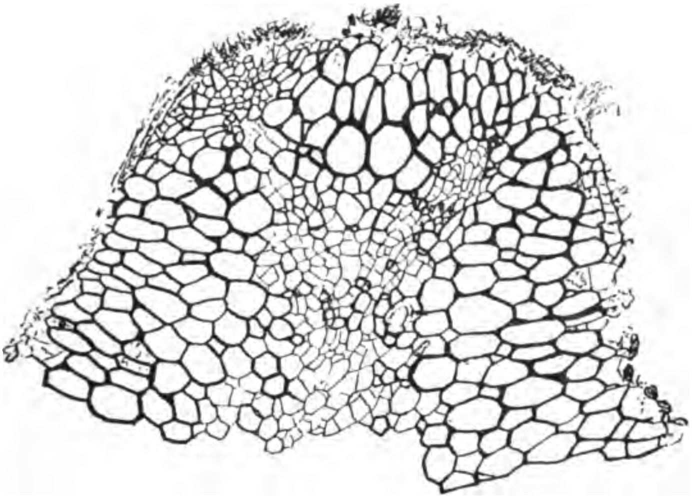

Fig. 7. *Zygopteris corrugata.* A double lobe of the stele showing the large metaxylem tracheids forming curved bands, and the central thin-walled parenchyma with scattered thicker-walled elements (tracheids), which pass into the lobes. Univ. Coll. Collection, K 32a. × about 35.

The leaf-trace departs as an isodiametric strand which divides tangentially as it passes through the cortex, the inner half becoming the stele of the axillary shoot, while the outer becomes the petiolar strand. The latter at first has the form of a tangentially extended band, as in *Tubicaulis* or *Grammatopteris*, but soon it spreads out at the ends and acquires the characteristic H-shaped form from which the name of the genus is derived (Figs. 8, 9, 10). The side-pieces of the H, which have their smaller elements (protoxylem ?) on their outer edges, are sometimes straight, but very often they are bent inwards so as to give the section of the strand the form of a double anchor. The xylem is often narrowed on each side at the points where the side-pieces join the central bar, so that they become almost (or in places quite) separated into four independent strands (Fig. 10). It is from these strands that the bundles supplying the pairs of branches on each side of the rachis of the frond depart. The two branches of each pair are evidently situated in the plane at right angles both to the ordinary plane of symmetry (vertical plane) and to the plane of the lamina of a typical fern frond[1] (horizontal plane, see Fig. 11). In *Z. Lacattii*, at least, one of the two branch bundles on one side of the rachis becomes much less important than the other,[2] while in this form and in *Zygopteris duplex* both branches divide again close to the base in the same plane (Figs. 12, 19).[3]

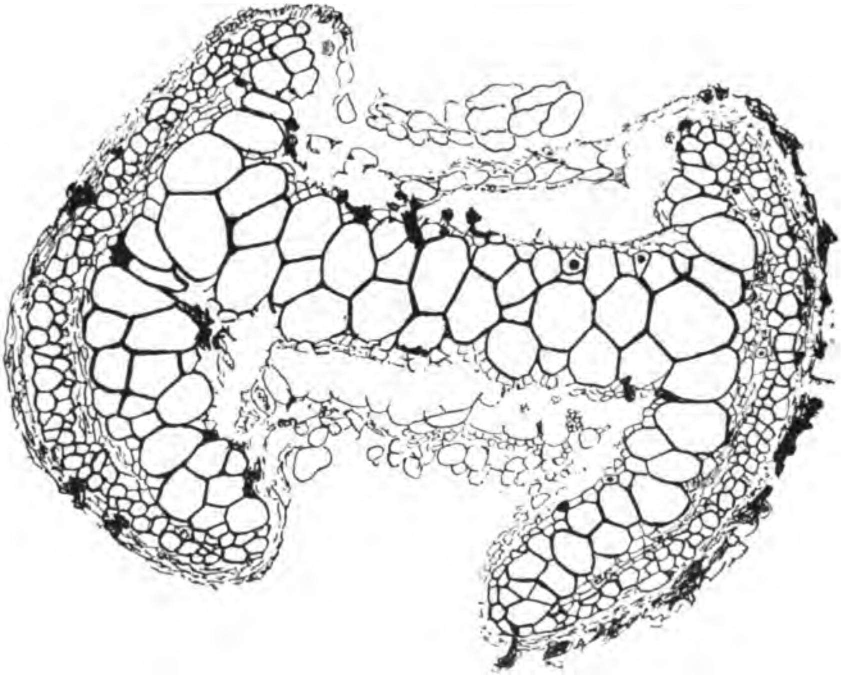

Fig. 8. *Zygopteris corrugata* (*Z. insignis*), petiolar strand. The side pieces of the characteristic H-shaped strand have each an external band of small tracheids joined to the large tracheids of the side piece at each end, and separated from them by an internal band of thin-walled parenchyma. The crushed tissue outside these external xylem-bands probably represents phloem and pericycle. Above and below the central band of xylem, large thin-walled elements probably representing sieve tubes of the metaphloem can be seen broken away from the central band. Outside these are narrow elements (pericycle and possibly protophloem), and outside these again a few of the large ground tissue cells have been indicated. Univ. Coll. Collection, K 33. × about 35.

In *Z. Bibractensis* and *Z. corrugata* (Figs. 8 and 9) the structure of the petiolar strand is even more complex. The cross-bar of the H is curved and there are two additional outer curved bands of smaller tracheids following the outline of the main "sidepieces" and connected with them only at the ends. The bundles supplying the branches of the frond arise from these outer bands.

---

[1] The plane of the pair of branches is actually *oblique* to the *vertical plane*, but may be considered theoretically as perpendicular to it.

[2] Williamson, '74. Plate LVIII., Fig. 48.

[3] Williamson, '74. Plates LV., LVI., Fig. 35

In *Z. duplex*, described by Williamson, the strand is hour-glass shaped in section, having a longitudinal furrow .at each end (Fig. 13). When branches are about to be given off the cusps on each side of this furrow reach out towards the middle line (horizontal plane of the whole strand) and are cut off from the strand, temporarily fusing with one another across the furrow and then again separating before passing out; so that here again we have a pair of bundles given off on each side of the rachis. In the *Diplolabis esnotensis* of Renault (Fig. 14) the strand is of the same general form, though it is more X-shaped, connecting the "*duplex*-type" with the H-shaped, and the branch strands are given off in essentially the same way.

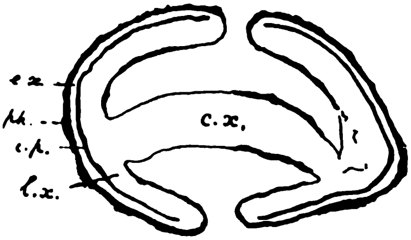

Fig. 9.

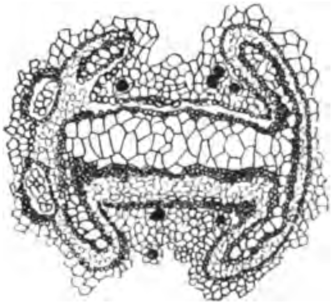

Fig. 10.

Fig. 9. *Zygopteris Bibractensis.* Diagram of petiolar strand, *c.x.*, central bar of xylem, *l.x.*, lateral bands of xylem, *e.x.*, external xylem of lateral bands, separated from the rest by internal parenchyma (*i.p.*), *ph.* crushed phloem, etc. After Scott.

Fig. 10. *Zygopteris Lacattii.* Strand of rachis showing departure of branch bundles. From Renault.

The vascular strands of the fronds known as *Stauropteris oldhamia*, Binney, closely allied to, if not actually to be included in the Botryopterideæ, are also related to this type. The fronds themselves are much branched and are apparently without lamina. We do not know if they are exclusively fertile fronds belonging to a dimorphic type or if they are true "trophosporophylls," but in some cases the ultimate branchlets, which arise in clusters, possibly by much condensed shortened dichotomies, end in sporangia. The xylem is cruciate, "the phloem filling up the bays between the xyem-arms, and sometimes extending to the middle so as to break up the wood" more or less completely (Fig. 16). The xylem is exarch and the branch bundles are given off from the protoxylems of the two xylem groups on one side of the axis (Figs. 16 and 17.) In the smaller branches the four xylem groups are reduced to three or two and eventually to one, the smallest monarch twigs ending in sporangia[1] (Fig. 18).

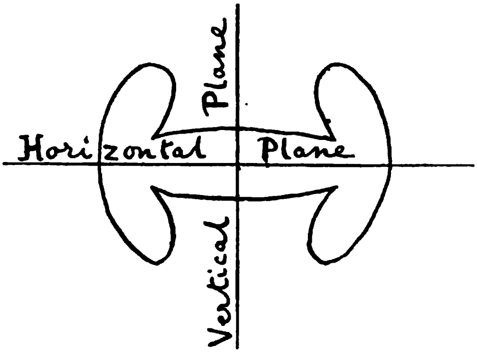

Fig. 11. Diagram illustrating the planes of symmetry of the frond of *Zygopteris* and allied types. The *vertical plane* is the plane including the axis of the stem, and is the normal plane of symmetry of the leaves of all the vascular plants. The *horizontal plane* is the plane in which the normal leaf is expanded, and which is also a plane of symmetry in *Zygopteris*. The *transverse planes* (the plane of the paper in this diagram is one) are those in which each successive pair of branches theoretically lies.

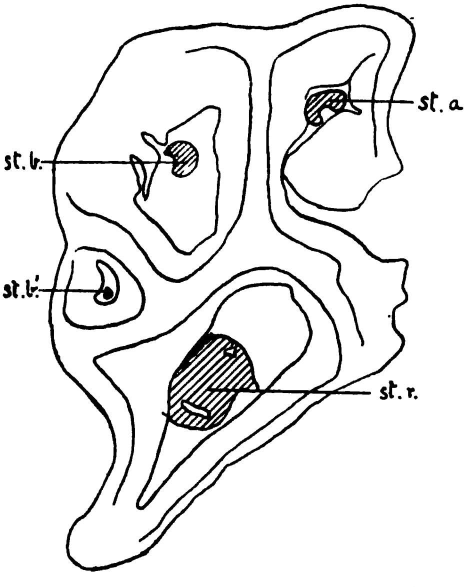

Fig. 12. *Zygopteris* ("*Rachiopteris*") *duplex*. Diagram of transverse section of rachis showing branching, *st. r.*, strand of rachis, *st. a.*, *st. b.*, strands of the pair of primary branches, *st. b.,'* strand of a branch of one of these. After Williamson.

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[1] Scott, '05. Dr. Scott has kindly allowed the publication of Figs. 15—18, which are taken from beautiful specimens that he was good enough to lend me.

All these "tetraxylic" types of petiolar strand present the striking character that in addition to the normal (vertical) plane of symmetry passing through the centre of the petiole and including the axis of the stem, they also tend to show bilateral symmetry about the (horizontal) plane perpendicular to this, *i.e.*, about the plane of the frond in *Zygopteris*. This is directly related to the fact that the frond in these types has pairs of branches lying in a plane perpendicular to the horizontal or plane of the frond, in what we may have called the transverse plane. Fig. 19, which represents a series of transverse sections through the rachis of *Z. Lacattii* is another illustration of this fact. In A the double-anchor-shaped strand of the rachis is seen having recently given off branches both above and below (in the figure) each of which divides into two *in the transverse plane*. The two strands so formed pass through the cortex (B) and enter an appendage or branch of the frond (C) which itself correspondingly branches in the same plane, each branch receiving a bundle. One of these however soon becomes less important than the other.[1] In *Zygopteris duplex*, as we have seen, essentially the same type of branching occurs (Figs. 12, 13.) Now this type of branching is fundamentally different from anything that is known in modern ferns, in

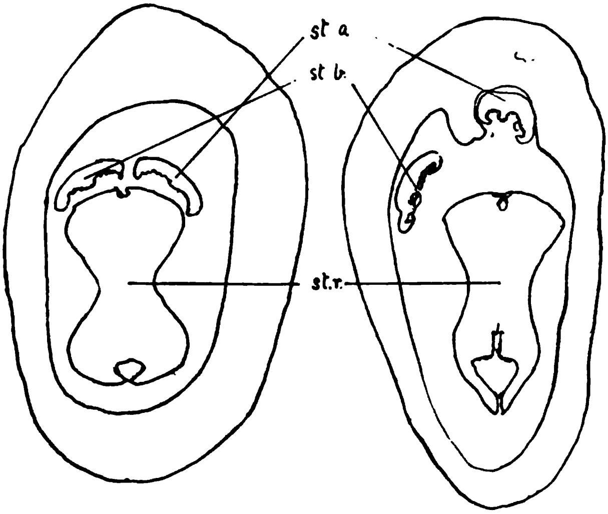

Fig. 13. *Zygopteris duplex.* Strand of rachis (*st. r.*), giving off branch-traces (*st. a.*, *st. b.*). The xylem and the limit between inner and outer cortex are outlined. The protoxylem is indicated in the concavities of the furrows and of the traces. The figures should be turned through a right angle to correspond with Figs. 8—11 and 14. Univ. Coll. Collection K 17, 18. × 7.

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[1] Williamson, '74. Plate LVIII., Fig. 48.

which branching is always strictly in the plane of the frond.[1] What is the connexion between the two? It seems that if a frond of the *Zygopteris*-type lost either its posterior or its anterior set of branches on both sides of the rachis, while the remaining set came to lie in the horizontal plane (as indeed they apparently tend to do, Figs. 12, 13B, 19c), we should have the ordinary type of fern frond, while with the disappearance of one set of branches the corresponding wings of the vascular strand would likewise disappear and the "double anchor" would be converted into a C. If it were the anterior branches which became aborted the concavity of the C would face outwards, away from the stem-axis, as in *Tubicaulis*, while if the posterior branches disappeared the C would lie with its concavity inwards, the normal orientation in the modern ferns. The probability of such reduction is rather suggested by the inequality of the twin branches on one side of the rachis in *Zygopteris Lacattii* as figured by Williamson, and perhaps also by the unequal development of the anterior and posterior wings of the rachis-strand often seen in *Z. insignis* (*corrugata*) (Fig. 9).

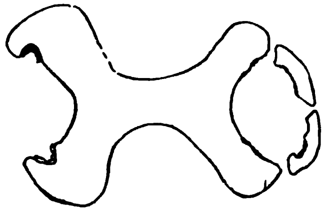

Fig. 14. *Diplolabis esnotensis.* From Autun. Strand of rachis giving off branch traces. Protoxylems as in Fig. 13. This type, which should probably be included in *Zygopteris*, has a strand intermediate in shape between *Z. duplex* and the ordinary types. Univ. Coll. collection, K 21. × 6.

It may be that *Stauropteris oldhamia* represents a type of frond-branching from which the *Zygopteris*-type is derived. Williamson described this frond as presenting "clusters of minute twigs," and it is easy to see from sections that an axis of the frond must have borne quadriseriate branches, which themselves branched in a similar manner (Figs. 16 and 17). The whole structure, even if it is to be regarded as the fertile frond of a plant with dimorphic leaves, must still have been extraordinarily unlike any other known type of fern frond. If now in such a case as this the whole frond tended to become flattened in one plane, and the main axis became relatively important, it is easy to see how the *Zygopteris*-type of structure might result. *Schizopteris*, the supposed leaf-impression of *Zygopteris* is a bipinnate, apparently normal frond, which has not yet been properly correlated with the structural material of *Zygopteris*, but it is possible to suppose either that one member of each pair became aborted, or that the pair of branches on each side became bent from the transverse into the horizontal plane, as happens for instance to the spirally arranged leaves of modern dorsiventral shoots in the flowering plants, under the influence of dorsal illumination.

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[1] A type of branching superficially similar to the *Zygopteris*-type seen in some species of *Gleichenia* and *Lygodium* is clearly shown by an investigation of the mode of branching of the strand of the rachis to be derived from the normal type by twisting of the branches through 90°.

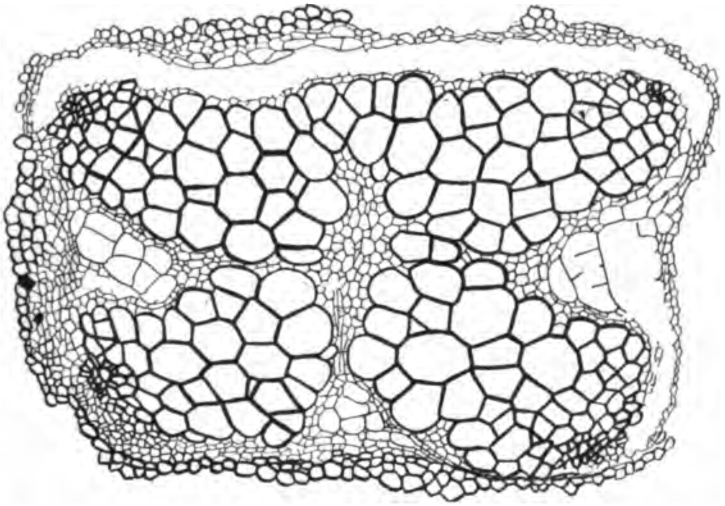

Fig. 15. *Stauropteris oldhamia*. Strand of an axis of the frond. The cruciate xylem is seen with its smallest elements (probably protoxylem) at the corners. The three groups of large thin-walled cells in the bays between the strands are probably large metaphloem sieve-tubes. Similar though smaller elements are seen broken away from the xylem a little to the left of the centre at the top of the figure. It is doubtful if the phloem is continuous round the angles of the wood. The inner cortex, not apparently very sharply separated from the small-celled pericyclic tissue, is indicated in places. Scott Collection. × 60.

It is not intended to suggest that *Stauropteris* was *necessarily* the ancestor of the *Zygopteris*-type, nor the latter of the *Tubicaulis*-type and of the C-type found in most ferns. But it seems probable that these four types have the homologies indicated and that the recent forms present a specialised and stereotyped type of organisation of the axis of the frond, which is only one of a number of types of organisation formerly existing, some of which reveal to us examples of branching all round the axis of the frond. This tendency to *radial organisation* of the frond may perhaps be regarded as a relic of the time when, according to our basal hypothesis, the structure of the fronds of ferns was but little differentiated from the structure of their stems.

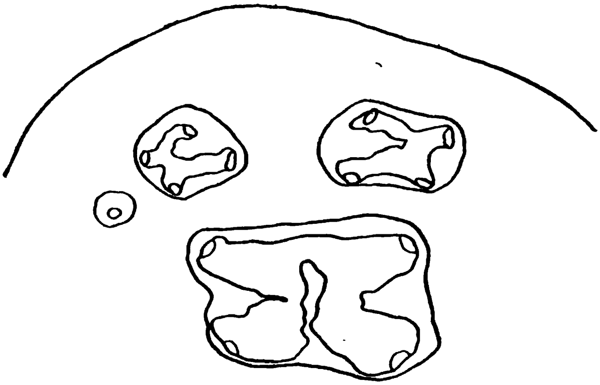

Fig. 16. *Stauropteris oldhamia.* Part of the axis whose main strand is represented in Fig. 15. Two tetrarch branch-traces are seen in the cortex with a small monarch trace to one side. × 20.

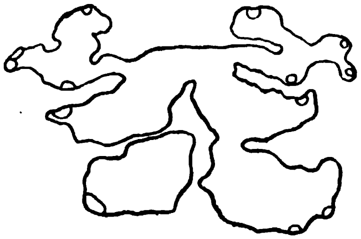

Fig. 17.

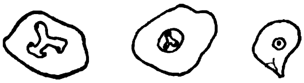

Fig. 18.

Fig. 17. *Stauropteris oldhamia.* Xylem of the strand of a large axis in the act of giving off branch traces: evidently an earlier stage of the condition shown in Fig. 16. Scott Collection. × 20.

Fig. 18. *Stauropteris oldhamia.* Tetrarch, triarch and monarch branchlets of the frond. Scott Collection. × 20.

The four masses of xylem making up the " cruciate " strand of the axis of *Stauropteris*, the two side pieces (which may be regarded as four wings) of *Zygopteris*, and the wings of the C-type are to be regarded as specialised parts of the rachis-strand developed to supply the demands of the branches or pinnæ; or, to put the same fact in another way, as the sympodial bases of the branch-traces.

This specialisation and partial isolation of conducting channels is a very general result of the progressive evolution brought about by increasing demands for conduction along certain lines. It may be traced for instance in the evolution of the stem-stele of *Zygopteris*, assuming, as seems probable, that it arose from a stele of the *Botryopteris*-type. The lobes of the stele represent the beginning of specialisation of leaf-traces, and this is combined with the enlargement of the periphery of the stele and the failure to develop many of the central tracheids, which become no longer necessary. This tendency is carried further in the genus *Anachoropteris* (Fig. 20) where the lobes of the stele become more prominent. In both genera the stele-lobe tends to become double (Figs. 6, 7, 20). This is probably to be interpreted as a basipetal development into the stem of the biseriate insertions of pinna-traces on the rachis-

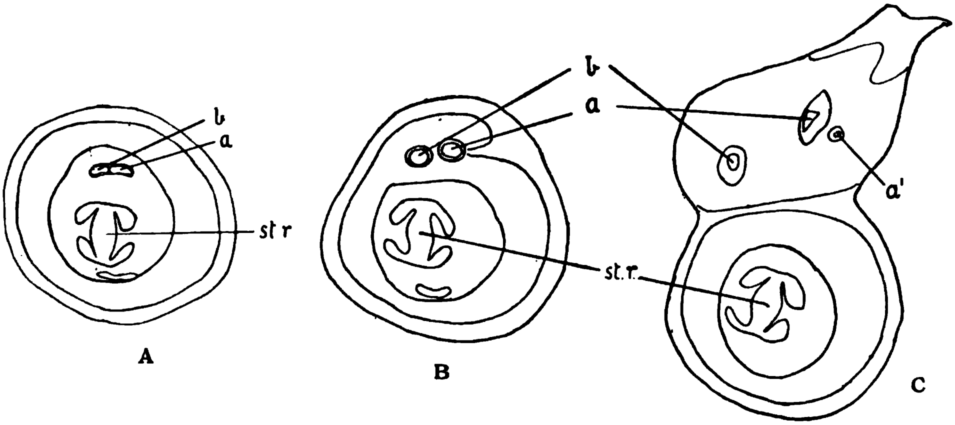

Fig. 19. *Zygopteris Lacattii.* Three serial sections showing branching, *st. r.*, strand of rachis, *a*, *b*, strands of the pair of branches, *a'* side branch of *a*. These figures should be turned through a right angle to correspond in orientation with Figs. 8—11. Univ. Coll. Collection, K 36a, b, c. × 4.

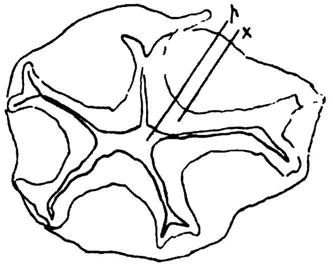

Fig. 20. *Anachoropteris Decaisnii.* Stem stele with star-shaped xylem (*x*) and pith (*p*), extending into the arms of the star.

strand of the frond. The leaf-trace of *Anachoropteris* (Fig. 21) is, according to Renault's account, at first a closed ellipse (A) which

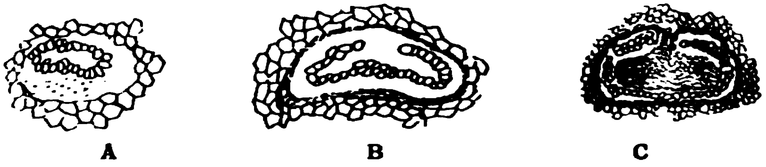

Fig. 21. *Anachoropteris Decaisnii.* Leaf-traces showing opening of ellipse probably on the abaxial side to form a C. From Renault.

afterwards opens (B and C) to form a tangentially extended C, apparently open on the abaxial side as in *Tubicaulis*. In *Asterochlæna* (Fig. 22) the lobing of the stele is even more marked, but the leaf traces apparently arise each from a single lobe, and are more of the *Grammatopteris*-type, so that this genus stands rather apart from the *Zygopteris-Anachoropteris* series.

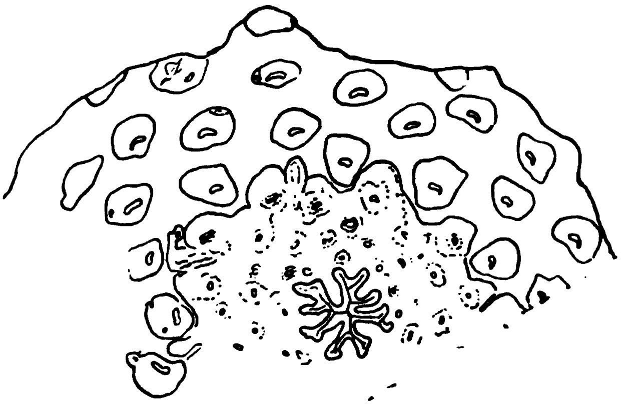

Fig. 22. *Asterochlæna laxa.* Part of transverse section of stem with bases of surrounding petioles, showing deeply lobed stele with pith extending into lobes and leaf-traces becoming slightly curved arcs in the petioles. From Stenzel.

Thus we see very clearly in the Botryopterideæ the beginnings of that tendency to basipetal phylogenetic development of the vascular system, from the transpiring laminæ into the axes of the frond and from the frond into the stem, which is really (apart from secondary thickening) the leading factor in the evolution of the general form of the vascular system throughout the higher plants.

LECTURES ON THE PHYSIOLOGY OF MOVEMENT IN PLANTS.[1]

BY FRANCIS DARWIN.

V.—THE SENSE-ORGANS FOR GRAVITY AND LIGHT.

ALL cases of stimulation depend on an influence of some kind affecting the protoplasm of the plant. Any arrangement which facilitates or intensifies the action in question may be called a *sense-organ.* Haberlandt writes[2] "I describe as sense-organs or perception-organs all those morphological or anatomical contrivances which serve for the reception of an external stimulus, and exhibit a more or less far-reaching correspondence between structure and function in this respect." Haberlandt's remarks are introductory to his treatise on the perception of contact-stimulus, in which the tropic element is not prominent; but they are also applicable to those contrivances by which plants orientate themselves in regard to stimuli such as gravity and light.

In the case of geotropism we want to know how (by what machinery) the plant perceives that it is not vertical. I have discussed this question in the Presidential Address to Section K at the Cambridge meeting of the British Association, 1904. But in order to give you the present state of the question, it will be necessary to repeat, by way of introduction, the essential part of what is there given. If a plant growing vertically is turned through 90° so that the unsupported stem projects horizontally, it is clear that strains and compressions will occur in the tissues of the plant which were not before existent. It is quite conceivable that such strains might constitute a stimulus to geotropism. But it is also clear that this is not the only means of geoperception, since plants supported throughout their length are nevertheless geotropic.

It has been suggested[3] that the change in hydrostatic pressure which would occur in a turgescent cell placed horizontally might originate a stimulus. Here again we can only say that such a thing is conceivable. A cell in the vertical position would have equal pressures on any two opposite points in the longitudinal cell-walls. But when such a cell is placed horizontal, the pressures on two supposed points. The validity of this theory not being easily the longitudinal walls (now horizontal) would be different at the tested, we may go on to the well-known *statolith theory*. The essence of this hypothesis is the conception that the stimulus is due to the differences in specific gravity of certain parts of the cell. The special form of the statolith theory which is connected with the names of Haberlandt[1] and Nĕmec is that a specialised form of starch grain supplies the heavy bodies in question. These "statoliths" lie freely in the cell and gravitate towards the physically lowest region. Thus in a vertical cell the pressure of the statoliths will be on the basal wall. When the cell is placed horizontally the starch will fall away from the basal wall (which is now vertical) and spread out in the lower lateral wall. In this way it is imagined that the pressure of starch grains on different parts of the cell-walls serve as signals informing the plant as to its angular position in space. Nor is this a vain imagining, because it has been absolutely demonstrated that in the case of the Crustacean *Palæmon* the power of orientation in regard to the vertical is dependent on the pressure of the statoliths (or otoliths) on the internal surface of the otocyst. This is a point of some importance, *viz.*, that the method of orientation believed to occur in plants does undoubtedly occur in animals. The truth of the statolith theory is not easy to prove or disprove. One obvious method is to inquire into the distribution of the above described free or "falling" starch. Our theory suggests a function for the statolith-starch that occurs in the endodermis, and it is significant that starch is only to be found here so long as the organ is growing, that is to say, so long as it is capable of geotropic curvature. It is especially striking that in Monocotyledons, in whose leaves starch does not occur, have falling starch in the endodermis.

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[1] A Course of Advanced Lectures in Botany given for the University of London at the Chelsea Physic Garden in the October term, 1906.

[2] *Sinnesorgane im Pflanzenreich*, 1901, p. 9.

[3] Pfeffer, Pflanzenphysiologie, Edition I., 1881, Vol. i., p. 330.

Then again the occurrence of falling starch in the cotyledons and not in the hypocotyl of *Sorghum*, *Setaria*, &c., agrees with the supposed distribution of geoperception in these seedlings. In the case of roots, the fact that there is a special patch of *statocytes*[2] in the root-cap appears at first sight to be in harmony with the localisation of geoperception in the root, but as I shall show there are some difficulties in the way of this argument. It is a striking fact that in *Viscum*, which appears to have lost the power of geoperception falling-starch does not occur. In the same way, statoliths are absent in the non-geotropic root of Ivy, *Hoya* and *Ficus*,[1] but are present in the geotropic roots of Aroids, as Tischler[2] has shown. The last named author placed aerial roots of Orchids horizontal and found that they curved downwards, but that they did not contain falling starch. This seemed an adverse fact until he discovered that the curvature in question was apheliotropic and that the roots showed no downward curve in the dark. Tischler gives other facts which are not in favour of the statolith theory. For instance the roots of *Pyrola* and also of *Pistia* are apparently ageotropic and yet possess falling starch. The case of tertiary roots of *V. faba* is interesting in this connection: they have usually been described as ageotropic, yet they possess statoliths. I was able to show that when the primary root is removed the tertiaries behave like normal secondaries and therefore need the apparatus for geoperception.

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[1] Haberlandt, Ber. D. Bot. Ges., 1900, xviii. Němec's paper appeared simultaneously in the same number. Both authors have published numerous later papers. I have not thought it necessary to give references for the many facts for which I am indebted to them.

[2] That is cells containing falling starch.

In a recent paper by Němec[3] some interesting facts are given, showing a general correspondence between the existence of movable starch and the capacity for geoperception in the Hepaticæ. Thus the sporogonium of *Aneura pinguis* has no statoliths and is apparently quite disorientated in the dark—showing that it is not guided by gravitation. On the other hand the vegetative shoots are strongly geotropic and have statoliths.

The sporogonium of *Pellia calycina* is feebly geotropic and the starch is but slightly movable. On the other hand the capsule-stalk of *Pellia epiphylla* has well developed easily movable starch and is strongly geotropic.

As making against our theory it must be stated that no statoliths have been discovered in Algæ or Fungi. But it must be remembered that Noll who first brought prominently forward the statolith theory does not believe in starch-statoliths, but supposes that minute particles in the protoplasm may play their part. And this may conceivably be the case in the lower plants.

The rhizoids of *Chara*[4] have bodies of unknown nature which fall to the lower end of the containing cell and may function as statoliths. The same may perhaps be said of the crystals which fall to the bottom of certain cells among the higher plants.

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[1] Haberlandt, Pringsheim's Jahrb. XXXVIII.

[2] Tischler in Flora, 1905, Vol. 94.

[3] Flora, 1906, Vol. 96.

[4] Giesenhagen, Ber. D. Bot. Ges. XIX. Němec mentions heavy bodies of unknown nature in the roots of *Trianea*, and in the stems of the Characeæ (Bull. Acad. Bohème, 1904).

The second section of evidence for the statolith theory is of an experimental character, and here great care is needed, as will be seen in the following instance.

I subjected *Setaria* seedlings to a high temperature, and this caused the starch grains to disappear and at the same time the seedlings lost the power of curving geotropically. This seemed a hopeful fact, but fortunately it occured to me to test their heliotropic powers, and it turned out that these had also been lost. Thus the loss of the statoliths must be considered merely as a symptom of the injurious effect of high temperature, and not as the loss of sense organs.

The same caution must be applied to certain experiments of Haberlandt. He found that plants of *Linum* growing out of doors in the early winter were not geotropic and had no statolith-starch. When brought into a warm room starch appeared and the power of geotropic curvature returned. Unfortunately the evidence that heliotropism was not simultaneously affected is not conclusive. The same must be said of Haberlandt's experiments in which the endodermis was removed by an operation with the result that the plants so treated lost their geotropic capacity.

Roots.

As already pointed out roots form the most serious difficulty of the statolith theory. In the first place we have no absolutely convincing evidence of the localisation of geoperception in the root tip, so that it may be urged that it is useless to investigate their statoliths. Still it is necessary to give some account of the difficulties that meet us.

Nemĕc shows (as others have shown) that a root, from which the tip has been cut, is no longer geotropic. Such roots recover the power as the wound heals, and what is especially interesting is that geotropism does not return with *general* symptoms of regeneration but with the actual appearance of statocytes. Nemĕc removed one millimetre from the roots of a number of *V. faba* seedlings: after fifteen hours some were found curving downwards, while others remained horizontal. On examining them microscopically it was found that the geotropic roots had statoliths, the horizontal ones had none. This seems at first sight good evidence for our theory. But a critic might say that the whole effect is one of shock which affects some roots more than others, and moreover that the shock not only prevents geotropism but also interferes with the regeneration of the statocytes.

Another experiment[1] of Němec's is the following:—

A transverse incision is made half way through a bean root close to the tip. The result is that a new root tip is formed at the basal lip of the wound, *i.e.* the one furthest removed from the root-tip, which acquires movable starch and finally replaces the old tip, which has meanwhile lost its statoliths. Twelve hours after the operation all the roots are geotropic because the old root-tip is still capable of functioning, not having lost its starch : seventy-two hours after the operation all the roots are also geotropic, but apparently for a different reason, *viz.*, because, though the old root-tip has lost its movable starch, the new root-tip has developed statoliths. Between these stages (twelve and seventy-two hours after the operation) there is a critical period, about sixty-six hours after operating, during which some but not all the roots are geotropic. This corresponds to the facts that the old root-tip has lost its starch, while the new tip has not had time to complete the formation of new starch-statoliths.

Czapek has made an ingenious point against the statolith theory. He showed that the roots of Lupine seedlings from whose roots half a millimetre has been removed still show the *homogentisinic* reaction when placed in the horizontal position. Now this reaction is according to Czapek[1] a proof that the roots are geoperceptive, and he adds that since the amputation has removed the falling starch-grains, the act of perception cannot have taken place by means of statoliths.

On the other hand it is denied by Němec that the removal of a half mm. takes away the whole of the starch, and he brings other facts to bear against Czapek—a discussion into which we cannot now enter.

Fitting objects to the statolith theory on the strength of his klinostat experiments, in which it will be remembered, he shows that, with an instrument rotating once a second, gravitation is continuously perceived by the plant. This is no doubt a difficulty but not, as it seems to me, an insuperable one.

On the whole it is not unfair to claim that the evidence for the theory has gained rather than lost strength since 1904.

Heliotropism.

What is here given is taken from Haberlandt's book[2] in which

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Ber. d. Bot. Ges. xxiii., 1905, p. 113.

he makes a highly ingenious suggestion as to how plants may be conceived to perceive the direction of incident light. His evidence is taken from the light-reactions of leaves, and to this part of the subject I shall confine myself.

Leaves (as I shall show in greater detail in my next lecture) have the power of placing themselves at right angles to incident light. This is effected by appropriate torsions and curvatures which are grouped together as *dia-heliotropic* or *transverse heliotropic* movements. In many cases,—possibly in the majority,—the act of perception is performed by the leaf-blade while the movement is confined to the stalk. In such plants it is clear that if sense-organs for light exist they must be sought on the leaf-blade. We should further expect that such organs would be found on the surface, more especially since the superficial layer of cells has as a rule no chlorophyll bodies which would obviously interfere with the optical behaviour of the tissue. It is, as a matter of fact, in the epidermis that Haberlandt finds the organs which, as having some resemblance to a primitive eye, he names *ocelli.*

The simplest kind of ocellus consists of an epidermic cell having a dome-like outer wall. Imagine one of these cells forming part of the epidermis of a horizontal leaf illuminated from above. As the light passes from the air to the fluid of the cell, it is refracted or bent; the cell in fact acts like a plano-convex lens and throws a spot of light on the basal cell wall. We have therefore the two elements of which the simplest eye can be imagined to consist, a lens and a sensitive protoplasmic membrane on which the light may be focussed.

We have imagined the leaf to be horizontal and under a top light, that is to say in a position of equilibrium. Now imagine the direction of illumination to be changed, by subjecting the leaf to oblique light. The consequence of this will be that in each of the epidermic cells the bright spot on the basal wall will be no longer central. We can imagine this acting as a stimulus and causing the leaf to move in such a way that it tends to become at right angles to the light: and when that position is actually reached the fact that the spots of light are once more in the centre of each of the basal walls will act as an inhibitory stimulus and the leaf will remain in a condition of equilibrium. It is certain therefore that domed epidermic cells may conceivably act as sense organs

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[1] Annals of Botany, Vol. XIX., p. 75.

[2] Lichtsinnesorgane der Laubblätter, 1905.

regulating the movements of the leaf in regard to light. What evidence is there that this is more than an ingenious hypothesis? In the first place there is no doubt about the existence of the spot of light. It is only necessary to remove by a superficial section the upper epidermis from an appropriate leaf,[1] and place the specimen under the microscope with the epidermal surface downwards. It is then to be illuminated from below, when a bright area surrounded by a dark border is clearly visible in each cell. On one occasion Haberlandt chanced on epidermic cells whose focal length was such that they cast a sharp image of an object standing near on to the basal wall of each cell. This remarkable specimen was photographed and is reproduced in Haberlandt's book. It is not suggested that it is of service to the plant that images of neighbouring objects should be thrown with this degree of sharpness onto the basal wall. The case is rather of interest as showing how good a lens may be made out of a vegetable cell. Before going on to describe some of the more interesting forms of ocelli it will be convenient to give an experiment of Haberlandt's which to my mind is very convincing of the truth of his theory. The experiment in question is simple enough, namely the submergence of the whole plant in water. If Haberlandt is right the submerged leaves should lose their power of orientation in regard to light for the obvious reason that submergence must prevent the epidermic cells functioning as lenses, since the water is of practically the same refractive index as the cell-sap.

This is what Haberlandt found to be the case, *viz.*, that the submerged leaves were apparently blinded and were at any rate unable to orientate themselves. It may be objected that the leaves were unable to move under water and that their behaviour had nothing to do with the "blinding" action of the water. This objection has, however, been met by Haberlandt in a manner which for simplicity's sake has been here omitted. Haberlandt's experiments with the leaves of *Tropæolum* are of some interest. They were found not to lose their powers of orientation when immersed, and this is what might have been expected, because they are well known to remain dry under water—protected by the layer of air entangled in their "bloom" of waxy particles. But if this coating of air is removed (by rapidly washing the surface in diluted alcohol) the *Tropæolum* leaf is wetted by water like any other leaf, and now ceases to respond to light.

I am inclined to accept Haberlandt's extension of his theory to the type known as "velvet leaves" in which the epidermic cells project as papillæ above the general surface. It is now suggested that this form of epidermic cell serves to prevent the leaf being "blinded" by the continuous rain of the regions where the plants in question chiefly occur.

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[1] For instance a leaf of *Begonia discolor*.

Other, and more specialised, types of what are believed to function as ocelli are described by Haberlandt. Some years ago Heinricher described in *Campanula persicifolia* some minute papillæ (for which he could suggest no function, apparently dwarfed or reduced hairs). It is certain that they might function as ocelli, for they produce a bright spot of light when the leaves are examined under the microscope as above described. This type is interesting in as much as the refractive quality of the ocelli depends on the rounded mass of silica deposited in the external cell walls.

In another well-marked type, that of *Fittonia Verschaffelti* (Acanthaceæ), the refraction, as in the first case described, depends on the form of the cell and the fact that it contains cell-sap. In *Fittonia* the epidermic cells are flat-topped and cannot function as ocelli, but among them are a number of two-celled trichomes of which the upper one has the form of a bi-convex lens, the broad lower stalk-cell serves as a support for the lens, and also doubtless supplies the protoplasmic membrane on which the spot of light is thrown. It is a remarkable fact that in *Impatiens mariannæ*, a plant belonging to a different Natural Order, closely similar ocelli occur.

Although Haberlandt's theory cannot be considered as absolutely established, it is deserving of every consideration. One feature of it is especially interesting, namely its broad general resemblance to the statolith theory. In both cases the directive element in the mechanism depends on the stimulus being applied to certain regions of the protoplasm lining the cell-walls. The organ recognises, as it were, that it is not vertical, or that it is not at right angles to the light, by a definite change in the position of the stimulated region.

A THEORY OF THE DOUBLE LEAF-TRACE FOUNDED ON SEEDLING STRUCTURE.

BY ETHEL N. THOMAS, B.Sc.
(University College, London).

[TEXT-FIGS. 1—4.]

EVER since the principle of recapitulation of the history of the race in the development of the individual became fully realized by biologists, and summed up in the well-known phrase "Ontogeny repeats Phylogeny," Botanists have endeavoured to use this instrument for disclosing the history of the ages, in the hope that it might prove as fruitful for them as it has been for Zoologists.

These expectations were, however, not fully realized, and the early attempts may be said to have resulted largely in disappointment. This is in a great measure due to the fact that the seriation of developmental stages in plants and in animals respectively is so little comparable, that great uncertainty arises as to what portion of the life-history of a plant should be included in the study of its embryology. Thus in addition to the more restricted aspects of embryology, great enthusiasm was shown for many years in the study of apices, meristems, and all growing regions, even of the later formed organs.

The early embryologists proper confined themselves to the study of the development of the ovum and of the differentiation from it of the first-formed members of the young plant. The minute comparative study of the early cell-divisions revealed so much inconstancy and variation that so far it has rendered little aid to phylogeny.

At the meeting of the British Association held in Liverpool in 1896, Dr. Scott drew attention to the lack of sustained effort in this direction, and also to the comparative neglect of the study of the later stages of development, during which organs and tissues are being differentiated. Since that time, *i.e.*, during the last ten years, much has been done to remove this reproach, and a new school of embryologists has arisen. In the Cryptogamic field, the work of Professor Jeffrey, Mr. Gwynne-Vaughan, Mr. Boodle, Mr. Tansley and Miss Lulham, and of Dr. Chandler has yielded interesting and important results.

The plant embryo may be said to superpose its stages of development in *space* rather than in *time*, producing more and more elaborate structure in the successively formed early members. This has its advantages and its disadvantages to the student of Plant Embryology, for while the early structure remains in its appropriate position, even in the mature plant—although, it may be, obscured by secondary changes—the stages of development are so spread out that the boundaries of embryology are ill-defined.

In Cryptogams these stages succeed each other in continuous development, but in Seed Plants there is a break in development due to the arrest of growth following upon the ripening of the seed, and corresponding to the interval between this process and that of germination.

The exact stage reached by the embryo in the ripe seed, before the arrest of growth takes place, varies considerably, but although a rudimentary plumular bud may be differentiated at the apex, the members of the embryo are characteristically the cotyledons, hypocotyl and radicle. Upon germination these members expand, and their tissues become further differentiated. There is theoretically, if not in all cases absolutely in fact, a line of demarcation to be drawn between this expansion and differentiation of members present in the ripe seed, and the production of new members from the plumular bud.

It is to the phase of development concerned with the establishment of the primary members and their maturation and internal differentiation, that the new Embryology is, so far, chiefly directed in Phanerogams. The features which appear to be of main importance for comparative purposes are the characters of the vascular system of cotyledons, hypocotyl and primary root, and the mode by which the positions of the vascular strands characteristic of the one, pass into those characteristic of the other.

Whether this phase corresponds to the first part of the continuously developing embryo of Cryptogams, and therefore, the cotyledons to the first leaves, and the hypocotyl to the basal portion, of the Cryptogamic stem, can only be decided on comparative internal evidence, although the importance of the results as bearing upon the wider phylogenetic issues, is to a great extent dependent upon this question. However this may be, Miss Sargant's work on Monocotyledons has shown that the study of this phase of development is of phylogenetic value, at any rate within the Phanerogams, and the increase of workers on the subject proves that it is felt to be a profitable field of research.

Mr. Tansley and I have been engaged in similar work on the seedlings of Dicotyledons and of Gymnosperms for several years past.[1]

I.—STRUCTURE OF DICOTYLEDONOUS SEEDLINGS.

The seedlings first examined were those of plants belonging to orders grouped according to Engler in the cohorts Ranales and Rhœadales.

The vascular system of the cotyledons, hypocotyl and root is very characteristic, and the mode of transition from cotyledons to root extremely simple, and with slight variation, and one or two exceptions, uniform throughout the genera and orders examined.

The striking feature in the cotyledon is the presence of a peculiar V-shaped bundle, which is obviously composed of two very definite halves, and has therefore been called a "double bundle." The apex of the V is occupied by a common group of protoxylem, while at the extremity of each arm is seated a phloem group (see text-fig. 1a).

DIARCH TYPE.

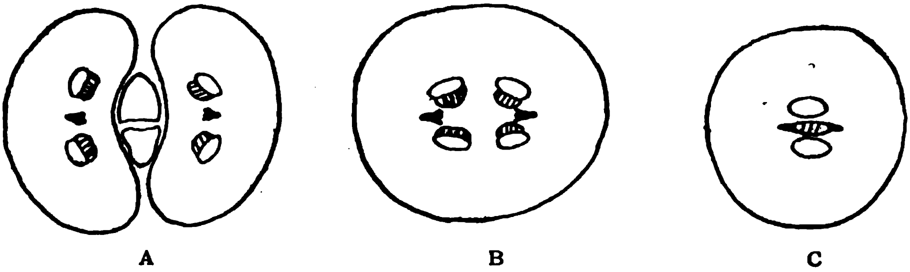

Fig. 1. Series showing transition features from cotyledons (*a*) through hypocotyl (*b*) to root (*c*). Protoxylem black; metaxylem hatched; phloem white.

At the base of the cotyledon petiole the protoxylem may be in such a position in relation to the rest of the bundle that the point of the V is either directed inwards V or outwards Λ, or the V is flattened out into a secant —·— with the protoxylem in the centre of the line. In any case the single protoxylem group from each cotyledon early assumes the external Λ position in the hypocotyl, and furnishes a pole of the diarch xylem-plate of the root. The alternating phloem groups of the root are derived by fusion of two phloem groups, one from each cotyledon. Thus the plane passing through the poles of the diarch root is the cotyledonary plane, while the phloem groups are in the inter-cotyledonary plane (see fig. 1c).

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[1] Tansley and Thomas. "Root structure in the central cylinder of the hypocotyl," NEW PHYTOLOGIST, 1904.

Tansley and Thomas. "The Phylogenetic Value of the Vascular Structure of Spermophytic Hypocotyls," Brit. Ass. Report, 1906.

Such a type of bundle and mode of transition is very widespread through the Dicotyledonous orders, and has been described by Gérard,[1] Dangeard[2], Sterckx,[3] Chauveaud[4] and Hill.[5]

When the present work was extended to other parts of the natural system it was found that the "double bundle" is sometimes represented by two quite separate bundles (*Ricinus*, *Quercus*, etc.)

The homology of the extreme forms is proved beyond question by the existence of a perfect series of intermediate cases. Further, the degree of approximation on the one hand towards a single bundle, and on the other hand towards two completely separate bundles, depends to some extent, in every case, upon the level in the cotyledons at which the bundles are examined.

The function of these central bundles, whether they appear as two widely separated entities, or so closely approximated as to to have the appearance of a single strand, is always the same, *viz.*, to form between them one pole of the root.[6]

In addition to the two central bundles or their "double-bundle" equivalent, there is frequently present a lateral bundle on each side of them, so that there are four bundles in each cotyledon (*Ricinus*, *Quercus*, *Fagus*) or the equivalent of four (*Casuarina*, *Polygonum*, *Liriodendron*, *Crataegus*, *Acacia*, *Medicago*, *Althaea*, etc.) ; see text-fig. 2a.

When the lateral bundles are large and important looking, they penetrate into the hypocotyl and unite with the corresponding bundle from the opposite cotyledon to form the alternating poles of a tetrarch root (text-fig. 2). Here again all intermediate stages have been found between this case and the presence of small laterals such as is customary in the type of seedling first described, in which they fuse with the central bundles high up in the cotyledon and have no influence upon the symmetry of the root.[1]

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[1] Gérard. "Recherches sur le passage de la Racine à la Tige." Annales des Sciences Naturelles, 1881.

[2] Dangeard. "Recherches sur le mode d'union de la tige et de la racine," Le Botaniste, 1889.

[3] R. Sterckx. "Recherches anatomiques sur l'embryon et. les. plantules dans la famille des Renonculacées" Mém. Soc. Roy. des Sci de Liège. 3e Sér, tom. ii., 1899.

[4] Chauveaud. "Passage de la position alterne à la position supérieure .... dans le cotylédon de l'Oignon." Bull. du Mus. d'hist. Nat., 1902.
Chauveaud. Sur la persistence de la structure alterne .... du Lamier blanc. Comptes rendus, 1904.

[5] T. G. Hill. "On the Seedling Structure of certain Piperales." Annals of Botany, 1906.

[6] In a few instances the bundles are grouped in diagonal pairs, composed of one central and one lateral, and the poles of the tetrarch root do not lie in the cotyledonary and inter-cotyledonary planes, but are formed in the diagonal planes. (*Achras*, *Quercus*, *Fagus*). Miss Winifred Smith first drew my attention to this arrangement in the Sapotacea

TETRARCH TYPE.

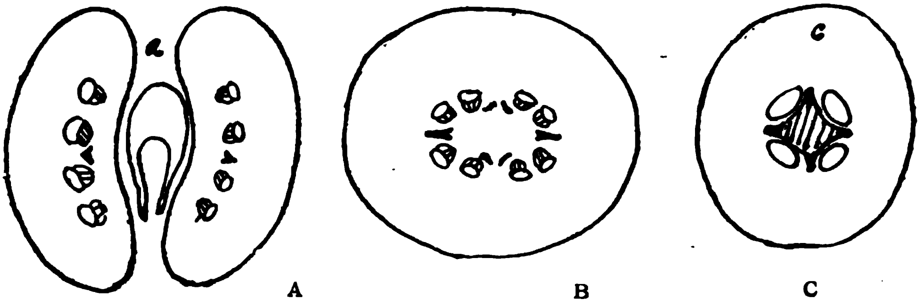

Fig. 2. Series showing transition features from cotyledons (*a*) through hypocotyl, (*b*) to root (*c*). Protoxylem black; metaxylem cross-hatched; phloem white.

A striking intermediate form is found in *Liriodendron tulipifera*, *Clematis Hendersoni* and in some Composites. Here the persistent, though slender, laterals penetrate into the hypocotyl, fuse with the corresponding bundles from the opposite cotyledon, and even begin to assume root characters but ultimately die out, so that the root is diarch (text-fig. 3).

INTERMEDIATE TYPE.

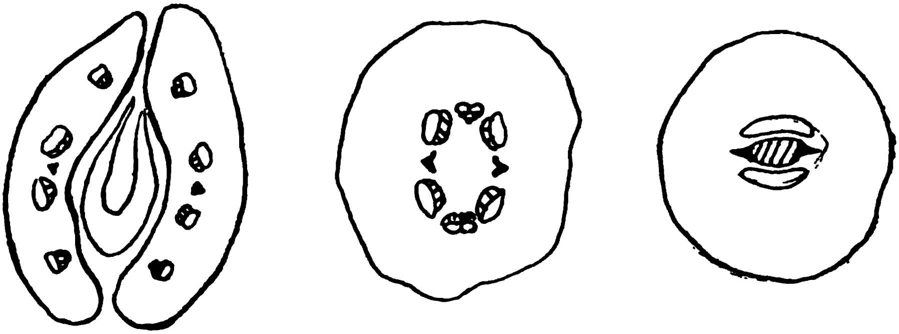

Fig. 3. Transition features in *Liriodendron*, etc.

II.—Structure of Gymnosperm Seedlings.

The publication of Matte's[2] paper in 1904, together with its interesting, but somewhat scanty description of the transition features of a few Cycad seedlings, convinced me of the importance of further examination of these forms. The account given of *Dioon edule* recalled very vividly many Dicotyledonous seedlings, while the description and diagrammatic figures of *Cycas siamensis* corresponded exactly to the features already found in *Liriodendron tulipifera.*

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[1] see footnote 6. p. 80.

[2] H. Matte. "Recherches sur l'appareil libéro-ligneux des Cycadacées." Caen, 1904.

Dioon has four bundles in each cotyledon, and these form a tetrarch root, exactly as in the Dicotyledons of this type. *Cycas siamensis* has also four bundles, but as in *Liriodendron tulipifera* the lateral bundles, although they enter the hypocotyl, fuse with those from the opposite cotyledon, and even begin to assume root characters, nevertheless die out, so that the root is diarch. It is impossible to avoid the conclusion that in both cases we have a stage in reduction from the tetrarch to the diarch type, particularly when it is taken in conjunction with other evidence to be considered below.

TETRARCH TYPE.

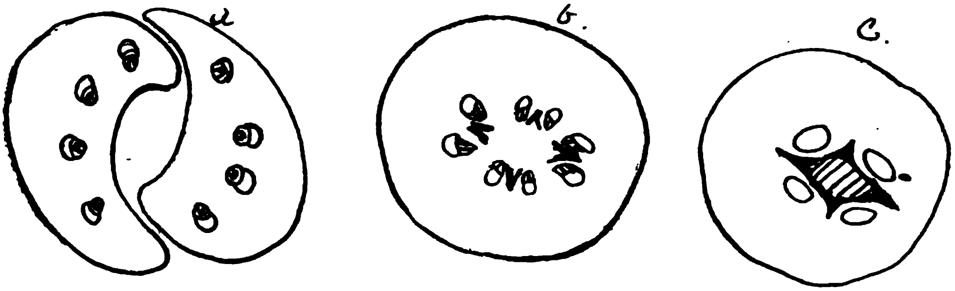

Fig. 4. Transition features in a typical Cycad.

A fair number of Cycads have now been examined, and all the available information gathered together. From this it appears that Cycad cotyledons are almost without exception destitute of a midrib, and have four or six bundles at their base; that the transition features take place so near the cotyledonary node that the hypocotyl is root-like in structure; and that the primary root is in most cases tetrarch, with a strong tendency to reduce near its apex to diarch. The genus *Cycas* would appear to be most abarrent, for while *C. revoluta* forms a tetrarch root, *C. siamensis* as described above forms a link between *C. revoluta* and *C. Rumphii,* which is diarch through the absence of inter-cotyledonary poles. Further *C. revoluta* may have its two central bundles replaced by a single one, which however plays the part of two.

Investigation of seedling structure in other Gymnosperm groups also proves of great interest.

The Araucarias approach the Cycads very nearly in some of their features, and the cotyledons have each four bundles, which towards the base approximate in pairs composed of one central and one lateral. They thus enter the hypocotyl from the diagonal corners. This grouping is also found in Dicotyledons (*Fagus, Quercus, Achras*), and almost certainly in some Cycads. Leaving out of account for the moment the variations met with in the very swollen forms, the hypocotyl bundles then form a diarch root by the approximation of the protoxylem groups in the cotyledonary plane.

The seedlings of the Coniferæ proper are in many cases complicated by the phenomenon of polycotyledony, of which a very interesting explanation—which the present work fullly bears out—was given by Mr. Hill at the York meeting of the British Association. Allowing for the complications thus induced, the polycotyledonous forms conform to the Coniferous type about to be described.

In the groups having two cotyledons, *viz.*, the Taxaceæ, Cupressineæ, and some of the Taxoideæ, the cotyledons each possess a single somewhat extended bundle, which forms a pole of the diarch root, precisely in the same way as does the double bundle of some Dicotyledons and the two separate bundles of other Dicotyledons and of Cycads.

III.—THE CASE FOR REDUCTION IN GYMNOSPERMS.

That the Coniferous forms show reduction on the Cycad type is a reasonable hypothesis on the grounds of the generally acknowledged antiquity and primitiveness of the latter group, but there is additional evidence which raises it to a reasonable certainty.

Ginkgo biloba, which has proved so interesting and important in other directions, is no less so in its seedling structure. Each cotyledon is provided at the base with a double bundle, the halves of which separate widely as they pass up the petiole, and in the lamina each proves to be itself double, *i.e.*, composed of a central and a lateral bundle. Thus we have the representatives of the four bundles characteristic of the Cycads, and grouped during one portion of their course as in the Araucarias and some Dicotyledons. The hypocotyl is characterized by a very high transition, giving rise to a diarch root, but it passes through a fugitive tetrarch stage.

The members of the Taxaceæ form a diarch root from an extended bundle, which in *Torreya*, recalls that of *Ginkgo* at the base.

The state of affairs in *Ginkgo biloba*, and the fact that the Araucarias may also show hexarch and tetrarch stages before assuming the final diarch form, taken in conjunction with the marked tendency to reduction seen in the Cycads, are very strongly in favour of the primitiveness of the tetrarch type, and the derivation from it of the diarch type by reduction, at any rate in the Gymnosperms.

That the types are not directly correlated with habit is very evident from *Araucaria*, *Ginkgo* and *Torreya*, the seedlings of which have the habit of a Cycad, with more or less completely Coniferous anatomical features.

IV.—THE CASE FOR REDUCTION IN DICOTYLEDONS.

Any attempt to assign taxonomic grade to a given character, is, at the present time, peculiarly difficult in the Angiosperms, for there is so little unaminity as to the relative primitiveness of the various alliances, that the evidence drawn from the antiquity of any one group, which was justly laid stress upon in connection with the Gymnosperms, can only be used with the greatest reserve among Angiosperms. Under such circumstances, there is considerable danger of arguing in a circle, and of assigning primitiveness to a character, because it is found in plants otherwise suspected of being primitive, and then using this character as fresh evidence of the phylogenetic position of the group. At the same time, if this danger be only properly appreciated, it should not prevent us from giving due weight to the coincidence of a supposed primitive character in a supposed primitive plant, if the primitiveness of both be also independently supported.

Such difficulties of necessity arise in the early stages of the minute and comparative study of groups, during which not only the characters likely to be of service in unravelling phylogeny are being determined, but at at one and the same time, the criteria by which they are judged are deduced.

One may regard the study of the Angiosperms as being largely in this stage, for, considered in relation to their great number, and the complexity of their structure, comparatively little exact work has yet been done on them. As far as seedling structure goes, it is felt that the number examined up to the present is very inadequate.

With this preface one may conveniently consider first, the evidence as to progression or reduction drawn from the distribution among the alliances of the two extreme types.

(a.)—Distribution of Types in Relation to Systematic Position of Plant.

The tetrarch type is characteristic of the Leguminoseæ, Rosaceæ, Euphorbiaeæ, Aceraceæ, Balsaminaceæ, Malvaceæ, and occurs in *Casuarina* and some of the Polygonaceæ and Amentiferæ.

Among the Sympetalæ it is found in the Convolvulaceæ, Sapotaceæ and Cucurbitaceæ.

The diarch type is, with the exception of the orders just named, characteristic of the Sympetalæ examined, and also of the Ranales, Rhœadales, Urticales, Piperales, Umbellifloræ, while it is found in some Polygonales and Centrospermæ.

It is obvious that the distribution of these types, as far as known, does not in itself point to any conclusion as to which is the more primitive. But this need not discourage one from drawing inferences from the distribution of the intermediate forms, nor from making use of other lines of evidence.

The *Ginkgo* of the Angiosperms is *Mirabilis Jalapa*, a member of the Centrospermæ, in which a tetrarch root is formed which reduces to diarch by suppression of the intercotyledonary poles. Mr. Hill informs me that the same thing occurs in *M. divaricata*, and also in *Allionia*, a plant belonging to the same order.

Among the Ranales the curious intermediate form seen in *Liriodendron tulipifera* and *Clematis Hendersoni* is found, while *Cassytha*,[1] a parasitic member of the Lauraceæ, is tetrarch.

The likeness between *Liriodendron tulipifera* and *Cycas Siamensis*, which almost certainly shows a stage in reduction, is interesting, for it is well known that the *Magnoliaceæ* have frequently been compared with the Cycads on other grounds.

Many of the Ranales possess two suspicious features (a) somewhat persistent laterals, (b) four phloem groups in the hypocotyl. These facts are suggestive, when we consider that of the neighbouring groups, the Rosales appear to be commonly tetrarch, while the Centrospermæ show reduction from tetrarch to diarch, and many of the Polygonales are tetrarch. Moreover, the members of the Ranales most likely to prove interesting have not yet been obtained.

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[1] Mirande. "Le dévelop, et l' Anat. d. Cassythacées." Ann. d. Sc. Nat. 9e Sér. Bot., tom. ii., 1905.

(b.)—Distribution of Types in Relation to Habit of Plant.

That the differences found in the anatomy of seedlings may be directly correlated with their habit very naturally suggests itself to one's mind. There is no doubt that habit has played an important part in the evolution of these types, but operating as an ancient differentiating force, so that its influence is seen, for the most part, over a large area embracing several families, and not in isolated genera and species. A secondary effect of habit can however be seen in individual members of families, as for instance in *Calycanthus*, which conforms to the general Ranales type, but the diarch root is only formed at the base of a long stem-like hypocotyl.

The intricate relation between habit and anatomy cannot be discussed here, but allowing that a certain broad correlation exists, one may consider whether this supports the case for progression or for reduction.

On several grounds one may perhaps assume that the primitive Angiosperm is likely to have been a plant with a fairly large, robust, slow-growing seedling, and therefore probably with the tetrarch type of anatomy. From this arose the more slender, quick-growing, herbaceous plant with its early production of perfect foliage leaves,[1] and reduced seedling anatomy. The original type, however, probably persisted in some families, possibly more or less correlated with the tree habit. Thus the Leguminoseæ, Rosaceæ, Aceraceæ, Sapotaceæ, Euphorbiaceæ, etc., are largely composed of shrubby and tree-like forms. Looked at in this way, it would be easy to understand why some plants, such as *Casuarina* and *Cassytha*, might have escaped anatomical reduction, on account of the insignificance of the early plumular traces. On the other hand, it would be difficult to account for them on the habit hypothesis, if tetrarchy be taken as a progressive character, for the effect could not well precede the cause, although anatomical reduction might lag behind modification of habit of hypocotyl, particularly if other necessary co-operating factors were absent.

(c.)—Internal Evidence.

From a careful consideration of the types as seen in Angiosperms and Gymnosperms, it appears easier to imagine the derivation of all the modifications found from a tetrarch than from a diarch form. The latter is generally associated with extremely definite and constant features, which suggest a certain stereotyped rigidity unfavourable to the evolution of new forms. The tetrarch type, on the other hand, particularly as seen in Gymnosperms, gives an impression of plasticity and variability, in the grouping of the bundles (two central, or one central and one lateral), and in the occasional appearance of diagonal tetrarchy, etc., which gives ample scope for the derivation of all the modifications seen.

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[1] It is always the intercotyledonary poles—and therefore those opposite the main plumular traces—which are suppressed.

The vestigial theory certainly appeals to one as a more plausible explanation of the intermediate form seen in *Liriodendron tulipifera*, *Clematis Hendersoni*, and curiously enough in some Composites, than the possible view which would regard it as a step in the progressive direction. It is difficult to see what functional advantage would accrue from such a very abortive attempt to form the intermediate poles of a tetrarch root, while it can very readily be understood, if regarded as an ancestral feature not completely eliminated.

Further, it is to be remembered, that where the root changes from tetrarch to diarch, it is always the basal hypocotyledonary end, *i.e.*, the older first formed portion, which is tetrarch, while the later apical end becomes diarch. It is reasonable to suppose that the modifying influences, due to the correlation of function with external conditions, would operate on the root and on the cotyledons, and affect least the hypocotyl, which is as a fixed point between two forces, only moved when these are in the same direction. Thus we find that in *Althaea rosea* and in many of the Leguminoseæ the four bundles of the cotyledon lamina become approximated to form a central group in the petiole, but the hypocotyl and root are nevertheless tetrarch. In *Mirabilis*, on the other hand, the cotyledon bundles are separate, and although the apex of the root is diarch, the hypocotyl remains tetrarch. Even in the most characteristically diarch families, if the laterals are persistent and independent, the top of the hypocotyl shows a more or less definite tetrarch stage (*Liriodendron tulipifera*, *Clematis Hendersoni*, *Lunaria biennis*, *Inula graveolens*).

But the hypocotyl is liable to certain modifications in response to its own particular function—that of support—and this modification is seen in both types. Where the cotyledons are epigeal, and the hypocotyl early bears a weight of foliage and has to provide for the insertion of numerous leaf-traces—as in many tree forms—the hypocotyl is stem-like in structure through the wide separation of the cotyledon traces, the protoxylems of which assume the endarch position (*Calycauthus*, *Linum*, etc., diarch ; *Acer*, *Ricinus*, etc., tetrarch).

(*d.*)—*Collateral Evidence.*

The very good case for reduction in Gymnosperms adds probability to the case for Dicotyledons, and further, Miss Sargant's work on Monocotyledons supports this view. She saw reason to derive all the modifications met with in the Liliaceæ (including diarch forms), and probably in all Monocotyledons, from the tetrarch type as seen in *Anemarrehena.* Here each of the two massive traces found in the single cotyledon is believed to represent the vascular system of an originally independent cotyledon, and each is shown to be a double structure. There is no doubt that each represents a four-fold cotyledonary trace massed together as in the petiole of the cotyledon of *Althaea rosea* and many other Dicotyledons. A tetrarch root is formed precisely as in the Dicotyledonous forms.

It may perhaps be mentioned here that the Gnetaceæ—suspected by some of Angiospermic tendencies—show an absence of midrib in cotyledons and foliage leaves, except in a few species of *Gnetum.*

The embryos in Bennettitean seeds are so beautifully preserved, that the paired bundles (usually six) of the cotyledons, are obvious and unmistakeable. Recent accounts of the Bennettiteaæ lead one to suppose, that among them, or in an allied group, will be found at least a candidate for the position of ancestor of the Angiosperms.

V.—BROADER PHYLOGENETIC CONSIDERATIONS.

If then the double bundle, which is so common in the cotyledons of Angiosperms, be the homologue of the two central bundles found in some Dicotyledons and in most Cycads, we have in the cotyledons of Angiosperms the reduced equivalent of the parallel series of paired bundles composing the foliar trace, not only of the cotyledons, but also of the foliage leaves of the older Gymnosperms.

Matte's work, previously referred to, was chiefly concerned with the elucidation of the vascular system of Cycadean leaves. He found that however complicated the vascular system of the petiole, its bundles were all derived from two initial strands. Worsdell[1] had shown this to be the case for the sporophylls and scale leaves. In all cases there is an absence of any central bundle throughout petiole and rachis, although the middle bundles may approximate during some portion of their course—or throughout in certain species—so as to simulate a midrib. The midrib found in the foliage leaves of many Conifers, is doubtless formed by the more or less complete fusion of the central pair, as was seen to be the case in Cycads.[1]

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[1] W. C. Worsdell. Vascular Structure of the Sporophylls of the Cycadaceæ. Annals of Botany, XII., 1898.

Professor Jeffrey,[2] who has drawn attention to the prevalence of the double leaf-trace in Gymnosperms. finds that the central strand of the Abietineæ is nearly always double in origin, at any rate in the early leaves.

The state of affairs seen in simple Cycad leaves (cotyledons, early foliage leaves, sporophylls) is precisely that found in the fossil allies *Poroxylon* and *Cordaites*, in which the double trace dichotomizes frequently as it passes up the leaf, and may do so, even before entering it. *Cordaites*, it will be remembered, combines Cycadean and Coniferous characters, so that it is interesting to find in it a form of nervation which is the basis of that of the modern Cycads and Conifers, and which is retained in its simplicity by some of the Araucarieæ.

The double leaf-trace of the extinct group of the Cycado-Filices is one of its most marked characteristics.

Dr. Scott in his "Studies in Fossil Botany" (1900) commented on the frequent occurrence of a double leaf-trace in the Cycado-Filices and the older Gymnosperms, and all the evidence brought to light since then goes to show that this character is more fundamental and widespread than was then supposed. The Gymnosperms and Cycado-Filices have been brought so close together during the last few years by the discovery of the seeds of the latter group, that we cannot now doubt that the paired parallel strands of the simpler Gymnosperms are the lineal descendants of the double leaf-trace of the Cycado-Filices. It is of considerable interest therefore to find the last remnant of the double leaf-trace in the cotyledons of Angiosperms. It furnishes another link to bind this puzzling modern group to the long and ancient series arising from a fern-like base.

It is not likely that any Ferns now known, either recent or fossil, give us much guide to the actual form from which the Cycado-Filices sprang. It is therefore not surprising that neither the Carboniferous Ferns (Botryopterideæ and Psaronius), nor the supposed primitive families (Hymenophyllaceæ, Gleicheniaceæ, Schizaeaceæ, Osmundaceæ) among living Ferns show an obvious double trace. Seedling stages of these families are, however, very little known. On the other hand the early leaves of the Ferns roughly classified as Polypodiaceæ—so far as they have been examined[1]—possess a double leaf-trace. The later leaves may have a four-fold trace, while the first one or two leaves usually show a single strand. The members of the Marattiaceæ and Ophioglossaceae (*Ophioglossum* not known) all show two separate bundles, or a twin strand, at any rate, in their early leaves. The twin strands in the first leaves of *Botrychium* are strikingly like the "double bundles" of the cotyledons of Angiosperms.

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[1] In *Cycas Seemanni* one cotyledon may have two central bundles, while the other has a single central bundle (Bower, 1884).

E. C. Jeffrey. Comparative Anatomy and Phylogeny of the Coniferales. Part 2, Abietineæ. Memoirs of the Boston Soc. of Nat. His., 1905.

It is just possible that the double trace of the Ferns has no direct connection with that of the Cycado-Filices. In the Ferns it is found in its most marked form in the advanced rather than in the primitive families. This may prove explicable, particularly when more information is available concerning the early stages. However this may be, it is very striking to find the character so prevalent in both groups.

The fairly universal presence of the double leaf-trace through the Fern-Gymnosperm series, and in a reduced form through the Angiosperms; together with its very frequent occurrence in modern Ferns, points to the existence of a common cause of a fundamental and primitive character Dichotomous branching at once suggests itself, as a primary and wide-spread phenomenon likely to have a bearing on the double leaf-trace, which is neither more nor less than an early dichotomy of the vascular system of the leaf.[2] Dichotomy is the characteristic mode of branching of the lower plants, and is widely recognised as the basis of many of the more complicated pinnate methods seen in the higher plants· Looked at in this way, the double leaf-trace appears as the vascular bifurcation corresponding to the dichotomous branching of the leaf. This dichotomy is obvious in the first leaves of many Ferns, but soon the dichotomy becomes unequal, so that a more or less completely pinnate form of branching takes its place. At the same time a definite petiole develops, so that the region of precocious dichotomy of the vascular system is much drawn out. This results in the presence of two strands throughout the petiole. In some cases a single strand is reformed, by the fusion in the petiole of the originally separate bundles, which open out again when the lamina is reached.

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[1] Chandler. Ann. of Bot., XIX., 1905.

[2] Professor Lignier's very interesting paper ("Equis. et Sphen. Leur origine filicinéene commune." Extrait du Bull. de la Soc. Linn. de Normandie. 1906) on the subject of primitive dichotomy—only recently come to my notice—has been of great service in the final formulation of this very similar hypothesis resulting from the seedling investigations described above, and which has been in process of elaboration for the last year or two.

Potonié[1] has drawn attention to the repeatedly dichotomous mode of branching of the fronds in Palæozoic impressions, and Oliver and Arber[2] agree that this is probably indicative of the foliage of the Cycado-Filices rather than of true Ferns. If this be so, it affords a ready explanation of the more obvious presence of the double trace in the Cycado-Filices than in the Ferns. The common occurrence of fusion in the petiole of Lyginodendron, of the originally separate strands of the leaf-trace, is very plausibly explained by supposing that the primitive early dichotomy of the leaf is delayed by the differentiation of a petiole. The similar fusion found in the early leaves of some Ferns has been referred to.

Dichotomy may then perhaps be considered the mode of foliar branching which probably obtained in the early fern-like groups from which the Cycado-Filices and the Ferns arose. Its influence is seen in the irregular dichotomy of the fronds of the Cycado-Filices, and in the dichotomy of the early leaves of modern Ferns. It may perhaps be connected with the splitting of the cotyledons, which is one of the causes of the polycotyledony of the Conifers, and which is also occasionally found in other groups It probably also directly or indirectly accounts for the double leaf-trace of the Fern and Fern-Gymnosperm groups, and it finds its latest expression in the "double bundle" of the cotyledons of Angiosperms.

In conclusion I wish to express my great indebtedness to Mr. Tansley for his generosity in suggesting that I should publish these results from our joint work. It is impossible to estimate the influence which the benefit of repeated discussions with him has had on the theoretical views here brought forward. My thanks are also due to him for much helpful criticism during the preparation of this paper.

It is hoped that a much more exhaustive and comprehensive account of seedling anatomy will be possible before long.

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[1] H. Potonié. Ber. deutsch. bot. Gez. XIII., 1895, etc.

[2] E. A. N. Arber. "On the Past History of the Ferns," Annals of Botany, 1906.

THE TAXOIDEÆ; A PHYLOGENETIC STUDY.

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[WITH PLATE I.]

I.—INTRODUCTION.

EARLY in 1904, at the suggestion of Professor F. W. Oliver, I began to make a study of the Taxoideæ. At that time the the minute structure and development of the reproductive organs of the group were not known with any completeness except in *Taxus*, but in the course of the last three years several papers have appeared on the subject, culminating quite recently in Professor A. A. Lawson's interesting study of *Cephalotaxus*, (see Literature Citations, 16, 17, 18, 19, 26). We are now acquainted with at least the main outlines of the reproductive processes of these plants, and a considerable mass of information has accumulated as to their floral morphology, anatomy, etc., so that it seems as if the moment has come to enquire what bearing this knowledge may have upon our ideas as to the phylogeny of the group. I have made some attempt to do this in the following pages. I should like to take this opportunity of thanking Professor F. W. Oliver for the help and encouragement which he has constantly given me in the study of the group. Before entering on any general discussion I have a correction to make and a few observations to record.

II.—OBSERVATIONS.

(a). *Torreya californica.* Torr.

I wish to begin these notes by correcting an error into which I fell in a paper on *Torreya californica* (17) published in this journal in 1904. I stated there that the division of the "body cell" nucleus of the pollen tube gave rise to two sperm nuclei *of equal size.* Since my paper was published an account of *Torreya taxifolia* by Coulter and Land (19) has appeared, in which the division of the body cell in this species is described as *unequal,* thus resembling that of *Taxus,* in which the functional male nucleus is greatly larger than the functionless one. The discrepancy on this point between my results and those of Coulter and Land, made me re-examine my preparations, and I have come to the conclusion that my statement of 1904 was incorrect. Pollen tubes were comparatively scarce in my material, and I chiefly based my statement on the two preparations represented in Pl. 8, figs. 17 and 18 of the paper referred to; I now think that the nuclei there figured were wrongly identified. The two nuclei which I interpreted as the second male nucleus and a vegetative nucleus I now regard as respectively the functional male nucleus and the smaller second male nucleus, while the nucleus which I labelled "$♂_1$." I now believe to be merely a vegetative nucleus. I particularly regret this mistake as I had in my possession at the time of writing the paper a preparation and sketch made by Mrs. Tansley in the previous year, in which the entry of the sperm into the archegonium was shewn, and the smaller size of the second male nucleus was distinctly indicated. This drawing Mrs. Tansley has kindly given me permission to reproduce (Fig. 1).

(b.) *Taxus baccata.* L.

The development of the reproductive organs of *Taxus baccata* has already been investigated with considerable completeness by several workers (Belajeff, 4; Strasburger, 6 and 18; Jäger, 7), but since microtome methods have not been applied to the more interesting stages I thought it might be worth while to re-examine the ovules. My thanks are due to the Director of the Royal Gardens, Kew, for allowing me to collect material during the summers of 1905 and 1906. I used chiefly Juel's fixative (2 grs. zinc chloride, 2 c.c. glacial acetic acid, 100 c.c. 45-50% alchohol) which seems particularly well adapted for Gymnosperm ovules, followed by Flemming's triple stain. My results on the whole have simply confirmed previous work. Apparently the presence of more than one embryo sac is fairly common in *Taxus* ovules; cases are described by Hofmeister (1), Jäger (7) and Thomson (21), and I have met with one such example in my 1905 material. The ovules which I examined were abundantly penetrated by pollen-tubes, whose great swollen ends often pressed the prothallus quite out of shape, and sometimes grew right down its flank. As might have been expected, the dates of the various stages of the ovular development given by Jäger for material grown in the neighbourhood of Zurich do not apply accurately to that collected in England. The division of the body cell, and fertilisation, which Jäger describes as occurring at the end of May or beginning of June did not take place in my 1906 ovules until June 18th. The actual division of the body cell seems never to have been figured, so I have shown it in Figs. 2A, B, C, D. These figures bring out the rather interesting point that the division itself is perfectly symmetrical, and it is only the great subsequent growth of the functional male nucleus which brings about the inequality.

Hofmeister (1) gives the number of archegonia in *Taxus baccata* as 5 to 8. Jäger (7) confirms this as the normal number, but says that he found cases of 9, 10 and 11. In my 1906 material I met with an embryo-sac containing 17 archegonia! Two archegonia sometimes occur with no intervening prothallial cells. I have not detected any trace of a ventral canal cell nucleus.

According to Jäger, wall-formation does not occur in the proembryo until 16 to 32 nuclei have been formed. My observations confirm this. One ovule contained 7 proembryos! Three of these were binucleate, two were 8-nucleate, one shewed 16 daughter nuclei still connected in pairs, and in the seventh there were 16 resting daughter nuclei, but still no trace of wall-formation.

III.—AFFINITIES AND PHYLOGENY.

According to the most recent classification of the Taxaceæ (that of Pilger, 15), this group is divided into three sub-families:—

1. Podocarpoideæ.
2. Phyllocladoideæ.
3. Taxoideæ.

Other authors however do not place *Phyllocladus* in a sub-family of its own; Coulter and Chamberlain (9) include this genus in the Taxoideæ, while Strasburger (2) attaches it to the *Podocarpus* group. The result of some observations on *Phyllocladus alpinus* (Robertson, 22) has been to convince me that the older of these two views more nearly expresses the true relationship, and that *Phyllocladus* is intermediate between the Podocarpoideæ and Taxoideæ, but with somewhat greater affinity for the former. The Taxoideæ are sub-divided by Pilger as follows:—

CEPHALOTAXEÆ.
Cephalotaxus,
TAXEÆ.
Torreya.
Taxus.

Ginkgo used to be included with the genus *Cephalotaxus* (cf. Veitch, 8), but modern work, especially the discovery of the motile sperms, has emphasized the uniqueness of the Maidenhair Tree among the Conifers, and its resemblance to the Cycads, and it has been removed from the near neighbournood of *Cephalotaxus* into an alliance of its own,—the Ginkgoales.

The relation of *Cephalotaxus*, *Torreya*, and *Taxus* to the other Conifers has been the subject of much controversy. According to our present imperfect knowledge of the geological history of the Coniferales, the Taxaceæ appear at a somewhat later period than the Abietineæ; more complete information however is needed before we can draw trustworthy deductions as to the history of the group.

There are two contrasting views as to the position of the Taxoideæ:—

1. *That the Taxoideæ are a group retaining relatively primitive characters* (Strasburger, 5; Coulter and Chamberlain 9; Worsdell, 10, etc.) Those who take this view commonly regard the Taxoideæ as descended from some group of the Fern-Cycad alliance.

2. *That the Taxoideæ are relatively specialised*, while it is rather the Abietineæ which should be regarded as a primitive group. (Jeffrey, 20; Thomson, 21; Lawson, 26.)

We will begin by considering the evidence for the first view.

The anatomy of the three genera offers some distinctly primitive features. More traces of centripetal xylem are found here than in any other family of Conifers. (For references on this point see Robertson 22, p. 263). Strasburger (5) has shewn that *Taxus* has no albuminoid elements in its secondary phloem rays, that is to say the secondary structure of the phloem is *not* more specialised than the primary structure. This character, which is shared by *Ginkgo* and *Araucaria*, he regards as an indication of primitiveness, contrasting with the specialised anatomy of the Abietineæ, in which the albuminoid cells of the secondary phloem are confined to the rays. Strasburger looks upon this anatomical evidence as a confirmation of his view that any explanation of the floral structure of the Coniferæ must start from the Taxads.

The large erect seeds of the Taxoideæ recall those of *Cycas* and *Ginkgo* in their macroscopic characters. Professor F. W. Oliver (14) who has worked out the structure in the case of *Torreya* and has compared it with palæozoic seeds, describes the vascular anatomy as peculiar and isolated among recent plants, and regards the seed as of a distinctly archaic type.

The stamens of the Taxoideæ, like those of Araucaria, are characterised by possessing more than two pollen sacs. This is probably a relatively primitive character, representing in a very general sense a stage between numerous pollen sacs, such as we find for instance in the Cycadales, and the definitely bisporangiate condition met with in such a Conifer as *Pinus*. But it is necessary to bear in mind that the evolution of the microsporophylls of the Gymnosperms is still very obscure; there are great gaps between the microsporophyll of the Cycad, with its numerous clustered sori on the lower surface,—the pinnate synangia-bearing microsporophyll of *Bennettites* (Wieland, 25, Fig. 87 p. 164),—the erect stalked cluster of pollen sacs of *Cordaites*,—and the stamen of any of the Coniferales.

The minute structure of the reproductive organs does not give much positive evidence for the idea that the group is a primitive one, except in a single point to which I am disposed to attach some importance. This is the mode of development of the proembryo (see Coulter and Chamberlain, 13). In the Cycads and *Ginkgo* and probably *Bennettites* (Wieland 25, p. 125 and Pl. XXX.) the fertilised egg nucleus divides repeatedly before any walls are formed; but in *Pinus* as soon as four nuclei are produced they become separated by walls. *Taxus* and *Cephalotaxus* recall the Cycadean condition in that no walls are formed until at least sixteen free nuclei have arisen by division from the fusion nucleus.

The mature embryo of the Taxaceæ has two cotyledons; a similar dicotyledonous condition prevails throughout the Cycads, *Bennettites*, and *Ginkgo*, while polycotyledony is characteristic of the Abietineæ.

A further point in favour of the view that the Taxoideæ are a relatively primitive group is the resemblance which exists between the female " flowers " of *Taxus* and *Cordaites*. To this point I will return later.

The most important arguments brought forward by those who believe that the Taxoideæ are specialised rather than primitive are concerned with the structure of the megaspore and the female gametophyte. Dr. R. B. Thomson of Toronto has recently drawn attention to the " megaspore membrane " of the Gymnosperms (21). In common with other authors he regards the Gymnosperms as ultimately descended from forms in which the megaspores were set free from the sporangium; in such cases a firm protective spore coat would obviously be of use, but it would lose its function in the later stages of evolution when the megaspore became embedded in the nucellus. Hence Dr. Thomson looks upon the megaspore membrane of the Conifers as a vestigial structure, retained in the more primitive forms and gradually lost in the more advanced. He finds that the megaspore membrane is present, associated with a tapetum which he regards as of sporogenous origin, in the Cycads, *Ginkgo*, and the Abietineæ, while it is absent or very poorly developed in the Taxoideæ. While admitting the possibility that the megaspore membrane may have the phylogenetic value which Dr. Thomson attributes to it, I should like to point out that it is by no means certain that it is not an adaptive character. The Cycads have a very large and watery prothallus and they are characteristically xerophytes, so that in their case the well-developed megaspore membrane may have an important protective function. Also the fact that according to Dr. Thomson's observations the megaspore membrane is always associated with a tapetum, suggests that it may have some significance in connection with nutrition.

There are two other points in the structure of the female gametophyte of Taxoideæ on which Professor A. A. Lawson has laid some stress in his study of *Cephalotaxus* (26), as showing that this genus "represents a very recent type of Conifer." The first of these is the absence of the ventral canal cell. In *Cephalotaxus* there is a ventral canal nucleus, but it is *not* separated by a wall from the egg cell, while in *Taxus* and *Torreya* even the nucleus occurs rarely or never. In the Abietineæ on the other hand a well-marked ventral canal cell is cut off. The second point is that "prothallial" nuclei are absent from the pollen grains of Taxoideæ, while they are present in the Abietineæ. Lawson concludes "If the retention of such evanescent vestigial structures as the prothallial cells in the pollen or the membrane of the ventral canal-cell has any phylogenetic bearing, then we have an argument in support of the primitive character of the Abietineæ as a group." Another point which might perhaps be brought forward is that the differentiation between the two sperm nuclei in *Taxus* and *Torreya* is a decidedly sophisticated character. All these arguments seem to me to carry considerable weight, and to show at least that the Taxoideæ have specialised a great deal along their own particular lines, but nevertheless I am disposed to think that the balance of evidence is in favour of the view that the Taxoideæ have retained a greater number of primitive characters than the Abietineæ. One point which Professor Lawson brings forward, the absence of prothallial cells in the pollen grains of Taxoideæ, may, as I have tried to show elsewhere, (Robertson, 16, p. 139) find its explanation in the almost universal association of the *winged* character of the pollen grain with the presence of prothallial nuclei. (For criticisms of this hypothesis see Seward and Ford, 24, p. 392 and Lawson, 26, p. 4.)

The problem of the relation of the three genera of Taxoideæ *to one* *another* is a very difficult one. The connection between *Taxus* and *Torreya* seems to be considerably closer than that between either of them and *Cephalotaxus*, while on the other hand *Cephalotaxus* shews clear indications of affinity with *Ginkgo*. As regards the minute structure of the reproductive organs, *Taxus* and *Torreya* agree in the inequality of the sperm nuclei, and the absence or rare development of the ventral canal nucleus, while *Cephalotaxus* resembles *Ginkgo* in the equality of its sperm nuclei and the presence of a ventral canal nucleus. A curious little anatomical peculiarity shared by *Cephalotaxus* and *Ginkgo* is the presence of a central resin duct in the pith.

The female "flowers" of the Taxoideæ differ a great deal from those of other Gymnosperms. In *Taxus* the ovules are each borne in an apparently terminal position on a short leafy axis known as the "primary shoot." They are really however lateral on the primary shoot, being produced at the end of a much abbreviated secondary shoot, arising in the axil of the uppermost bract of the primary shoot. The growing point of the primary shoot is pushed to one side, so that the ovule seems to be terminal on it. Fairly often the *two* uppermost bracts of the primary shoot are fertile and in such cases the morphology of the structure is much clearer than in the reduced and more normal form (Figs. 4A and B). *Torreya* closely resembles *Taxus* (Figs. 5A and B). *Cephalotaxus* bears its female reproductive organs in cones, and though superficially very unlike *Gingko*, can really be more closely homologised with this archaic Gymnosperm than with the other Taxoideæ. The cone consists of a number of leaves each with two erect ovules in its axil.

Celakovsky's view as to the morphology of the female "flower" in the Taxoideæ, which is clearly expounded by Worsdell (10 p. 641, etc.,) seems to me to be far better founded and more luminous. than the other hypotheses that have been put forward. According to this view "the primary shoot of *Taxus* and *Torreya* . . . . is the homologue of the entire plant of Cycads and the brachyblast of *Ginkgo*; the secondary shoots are the homologues of the Cycadean cone and the ovuliferous axis of *Ginkgo*." The cone of *Cephalotaxus* is regarded as corresponding to the "primary shoot" of *Taxus* or *Torreya*, or to an aggregate of the ovuliferous axes of *Ginkgo* with their subtending leaves. The belief that *Ginkgo* and *Cephalotaxus* can truly be homologised on these lines has been strengthened of late years by additional observations on abnormal "flowers" of the two genera. Spiess (12) has found in both cases that when more than two ovules are present the extra ones are arranged decussately with reference to the normal pair.

In nearly all the points in which *Taxus* and *Torreya* differ from one another, *Taxus* is the less specialised, but in the structure of the mature seed the reverse seems to hold good. Professor F. W. Oliver (14) says of the seed of *Torreya*, "In the apparent retention of old features it exceeds either *Taxus* or *Cephalotaxus*." It is possible that the comparatively small size of the *Taxus* seed and its coloured aril (said to be attractive to birds) may have something to do with its wide distribution, while on the other hand *Torreya* and *Cephalotaxus* may partly owe their restricted habitats to the handicap of their cumbrous seeds. The radially symmetrical peltate stamens of the Yew, with their numerous pollen sacs, are represented in *Torreya* by dorsiventral stamens bearing four pollen-sacs on the lower side. That this is phylogenetically a case of reduction is strongly indicated by Coulter and Land's interesting observation (19) that the dorsal resin cavity in the stamen of *Torreya taxifolia* is formed ontogenetically by abortion and fusion of three rudimentary sporangia. The number of archegonia shows reduction as we pass from *Taxus* to *Torreya*. In the Yew ovule there are normally five to eight, but the number may rise to seventeen, whereas in *Torreya californica* three are commonly found, and in *T. taxifolia* only one. Again, the development of the proembryo of *Taxus* is less specialised than that of *Torreya*; *Taxus* produces sixteen to thirty-two free nuclei before forming cell-walls, while in *Torreya* wall formation is initiated at the four-nucleate stage.

The morphology of the female flower of *Taxus* and *Torreya* is also best explained on the view that *Torreya* is one degree more specialised than *Taxus*. In the case of *Taxus* the so-called "primary shoot" bearing bracts arises in the axil of a foliage leaf, while from the axils of the two uppermost bracts on this shoot secondary axes arise, each bearing three pairs of bracteoles and terminating in an ovule (Fig. 4). One of the secondary axes commonly aborts. In *Torreya* we meet with precisely the same arrangement, except that the axes are telescoped down, the number of scale leaves is reduced, and two secondary axes are normally, instead of occasionally produced (Fig. 5). The erect ovule placed terminally at the end of a secondary bracteole-bearing axis, which itself arises from a primary bract-bearing axis produced laterally on an axis of higher order, exactly recalls the arrangement described by Renault (3) for *Cordaianthus*, the female " flower " of the palæozoic Gymnosperm *Cordaites* (Fig. 3). *Taxus* is somewhat reduced from this type, in that the growing point of the primary shoot aborts after producing a certain number of sterile bracts, and either one or two ovule-bearing axes, whereas in Cordaites it produces, besides sterile bracts, *several* ovuliferous secondary axes, and then (instead of being reduced to a little barren cone) continues its growth and produces some more leaves, Fig. 3 (see also Renault 3, Pl. XV, Figs 1 and 3).

The morphology of the male " flower " of *Cordaites* is obscure, but it seems clear that the pollen-sacs were borne in an erect tuft at the end of a slender pedicel. The pollen-sacs of *Taxus* on the contrary are pendulous, but they resemble those of *Cordaites* (Renault 3, Pl. XIV., Fig 2), and differ from those of all other Gymnosperms in their radial symmetry with respect to the pedicel that bears them.

There seems to be no doubt that *Cordaites* was descended from ancestors belonging to the Fern-Cycad alliance. We have anatomical evidence for this in the structure of the stems of *Pitys*, a tree from the lower Carboniferous. Dr. Scott (11) regards it as a primitive member of the Cordaitean family, but with mesarch strands of primary xylem. In Dr. Scott's words, " The *Pitys* trees appear to afford a new link, as far as stem structure is concerned, between the Cycadofilices of the family Lyginodendreæ and the true Cordaiteæ." The seeds of *Cordaites* are said to " shew a marked parallelism with the ovules of recent Cycads." (Oliver 14).

Between the dying out of *Cordaites* at the top of the Palæozoic and the appearance of the Taxaceæ in the Cretaceous, there is a considerable gap in point of time, which may conceivably be bridged later on by the discovery of intermediate types.

CONCLUSION.

The evidence which we have been considering seems to point to the conclusion that the Taxoideæ are a group retaining many relatively primitive characters, though considerably specialised along their own lines. Phylogenetically they may be regarded as an offshoot from the Cordaitean stock, which is itself a branch of the Cycadofilicinean plexus. This descent is indicated by the marked resemblance of *Cephalotaxus* to *Ginkgo*, and of *Taxus* to *Cordaianthus*.

The relation between *Cephalotaxus* and *Ginkgo* has long been recognised, and Dr. Scott (23), has pointed out that *Ginkgo* thus forms a bond uniting the Taxaceæ to the Cordaitean phylum.

It seems, however, not impossible that there is an even more direct connection between this phylum and the Taxaceæ—a connection indicated by the fact that the *general morphology of the female "flower" of* Taxus *more closely recalls that of* Cordaites, *than that of any other known plant.* I do not of course intend to suggest that *Cordaites* is actually the direct ancestor of *Taxus* (from which it differs in a number of important points), but I think that there is reason to suppose that *Cordaites* and *Taxus* are descended from the same primitive stock, and that *Cordaianthus* gives some idea of one of the stages passed through by the female "flower" of the Taxoideæ in the course of its evolution towards the reduced and specialised forms of the present day.

⁂ Since this Paper was written my attention has been called to a memoir which I had overlooked, "Fertilization and Embryogeny in Cephalotaxus Fortunei," W.C. Coker, Bot. Gaz. XLIII., Jan., 1907. The observations in this paper are in agreement with those of Professor Lawson, published in the Annals of Botany for the same month, except that the author reports *inequality* of the sperm cells.

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EXPLANATION OF PLATE I.,

ILLUSTRATING MISS AGNES ROBERTSON'S PAPER ON THE TAXOIDEÆ.

Fig. 1. *Torreya californica*. Fertilisation stage. Egg cell (*e.c.*) and pollen-tube (*p.t.*) from longitudinal section of ovule gathered September 17th, 1902, shewing entry of functional male nucleus (♂$_1$). The second male nucleus (♂$_2$), distinguished by its smaller size, remains in the rear of body cell (*b.c.*) The egg nucleus (♀) and the remains of two neck cells (*n.c.* and *n.c.n.*) are shewn. (Preparation and drawing by Mrs. Tansley).

Fig. 2, A, B, C, D. *Taxus baccata*. Stages in the division of the body cell. *v.n.*, vegetative nucleus. From sections of ovules gathered June 18th and 21st, 1906. (× about 500).

Figs. 3, 4, 5. Comparison of female "flower" of *Cordaites, Taxus and Torreya*. *o*, ovule; *a*, arillus; *b*, bract; b^1 bracteole; *g p.*, growing point; *l*, leaf subtending primary shoot; s_1, primary shoot; s_2, secondary shoot.

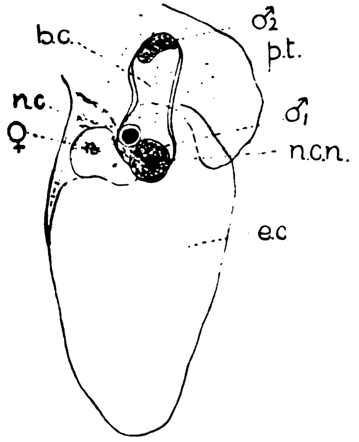
Fig. 3. Diagrammatic longitudinal section through the "primary shoot" of *Cordaianthus Williamsoni* (after Renault.)

Fig. 4A. Diagrammatic longitudinal section through "primary shoot" of *Taxus baccata*, illustrating a case in which the second ovuliferous axis (which usually aborts) has developed. (From a preparation by Miss T. L. Prankerd.)

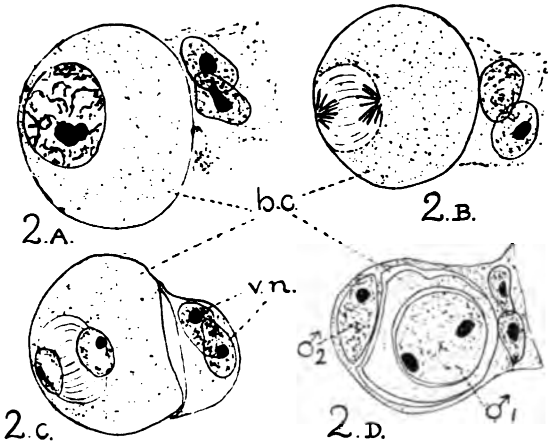
Fig. 4B. External view of a biovulate primary shoot of *Taxus baccata*, cf. Fig. 4A. (after Pilger.)

Fig. 5A. Diagrammatic longitudinal section throngh the "primary shoot" "of *Torreya californica*.

Fig. 5B. External view of shoot of *Torreya californica* with biovulate primary shoot in axil of leaf *l*, cf. Fig 5A.



TORREYA



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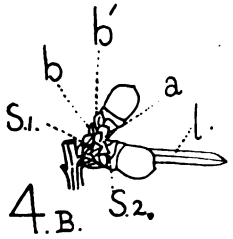

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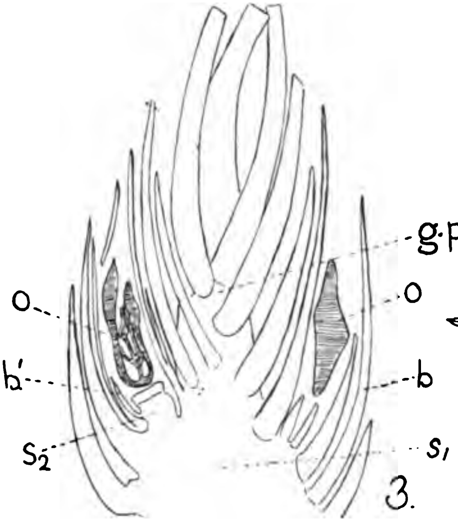

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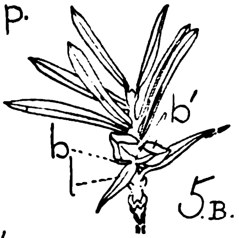

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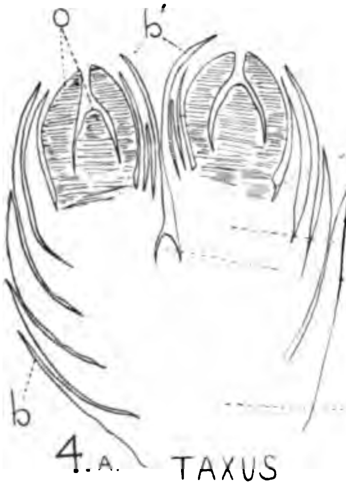

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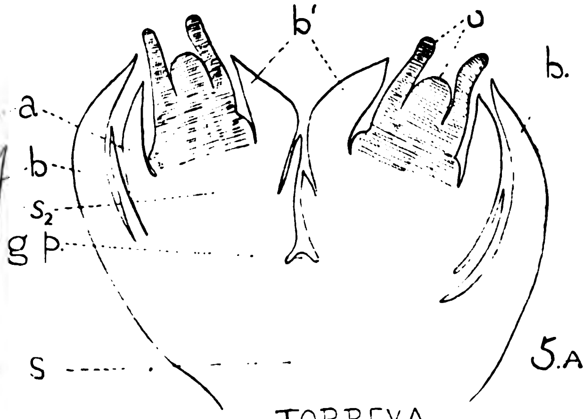

5.A

TORREYA

THE CENTRAL COMMITTEE FOR THE STUDY AND SURVEY OF BRITISH VEGETATION.

THE progress of the work of this Committee may be summarised, as in previous years, (see New Phytologist, January, 1905 and December, 1905), by giving some abstracts from the Minutes for 1906. The principal meetings, held in London on March 24th, and in the Botanical Laboratories of the University of Manchester on November 24th and 25th, were well attended A special meeting was called at York during British Association week to deal with some urgent business. Outdoor excursions, conducted by members familiar with the respective districts, took place into Surrey in March, and into Derbyshire in August. The membership has been increased by two, but it has suffered the loss of Dr. Marcel Hardy, who, after completing an important primary survey of the greater part of the North of Scotland, has sought in Mexico a wider sphere for studies in vegetation.

Whether one considers the organisation as a whole or the work of individual members, the past year has been one of distinct progress. The numerous communications, especially at the autumn meetings, indicate that members are all engaged on original research on vegetation, and that each one has problems more particularly his own. The Committee as a whole has considered several important questions of a technical character, but on which it is as yet too early to arrive at final conclusions. The chief items of interest may be summarised in groups.

Publications. Three Papers have been published by members during the year, and each one deals with a different aspect of Ecological Botany. "The Ecology of Woodland Plants in the Neighbourhood of Huddersfield" by Dr. T. W. Woodhead (Linnean Soc. Jour.—Botany, Vol. 37, October, 1906) is a detailed study of the vegetation of an area which has previously been treated in a "primary survey"; a review of the work has already appeared in these pages (Vol. V., November, 1906). "The Geographical Distribution of Vegetation in Somerset," by Mr. C. E. Moss, is an addition to the series of primary surveys of British vegetation, especially interesting because it is the first which deals with the vegetation of the South of England; a review will be found in a recent number (New Phytologist, February, 1907). The systematic investigation of peat deposits has been advanced a stage further into the Scottish

Highlands by Mr. F. J. Lewis's latest memoir (Trans. Roy. Society Edinburgh: Vol. XLV.).

Collection of Photographs. An excellent arrangement has been effected with the British Association Botanical Photographs Committee, whereby all botanical photographs collected either by that Committee or by this (the Survey) Committee may be consulted by anyone. The joint collection is to be lodged at University College, London for reference, while a duplicate collection, at Manchester and Cambridge will allow a selection of photographs to be borrowed by those who cannot consult the main one. A catalogue is in preparation for general distribution, which will be obtainable from Professor F. E. Weiss (University of Manchester) or Mr. A. G. Tansley (Botany School, Cambridge). Although still of course very incomplete, the collection includes many photographs of botanical subjects both at home and abroad.

Publication of Maps. Means for improving vegetation maps frequently come under discussion, with the result that proposals are now under consideration which, if effected, will do much to remove the lack of uniformity in the maps hitherto published, and will considerably reduce delay in the issue of memoirs.

Colour Scheme for Vegetation Maps. The progress of map surveys over fresh portions of Britain has led to the identification of new ecological groups not represented on the earlier maps and consequently not provided with distinguishing colours. The Committee felt that it was desirable to use allied series of colours for vegetation series which were allied ecologically. After careful consideration to which several Members devoted much time, a scheme has been drawn up which has been adopted and will be published at a later date.

It was also decided that further characteristic signs and symbols, and methods of hatching, stippling, &c., could profitably be utilized, and the Secretary was instructed to write to each member of the Committee for suggestions of this nature.

Communications by members have become a distinguishing feature of the Meetings, and as these are followed in each case by discussion and criticism, they are of service both to the author and to his audience. It is natural that the Autumn Meeting, following on a season of out-door work, should produce the greater number of communications, and at Manchester a long list of observations and results was laid before a Meeting from which only two members were absent. Mr. F. J. Lewis summarised his latest observations on Peat deposits, the results of three months' work in the Shetlands and the North of Scotland, including Rannoch Moor and several parts of the Grampians. The results conform to, and amplify, those of previous years, already published. The whole investigation has yielded most valuable results from the thorough and systematic manner in which it has been conducted, and in contrast to the former fragmentary and in many cases untrustworthy accounts, those of Mr. Lewis mark distinct progress in the knowledge of British Peat deposits.

Sections of peat examined on the Pennines near Halifax were described by Mr. W. B. Crump. In each case the peat was mainly composed of the remains of *Eriophorum* (and in two sections *Sphagnum*), *Calluna* being present somewhat sparingly in certain layers; the peat of this district seems therefore to have been formed under uniform conditions. Remains of Oak and Hazel were identified up to 1,100 feet, while Birch occurred at 1,250 and 1,400 feet, in all cases near streams. The water-content of peat was also examined, and results indicate that the deep peat of the *Eriophorum*-moor, so extensive in this area, has a larger water-content than the shallow peat of the *Calluna* moor; also that under varying seasonal conditions the percentage of water tends to remain nearly uniform.

Mr. R. Lloyd Praeger communicated recent observations in Ireland. The steep rocky island of Lambay off the coast of County Dublin has come into possession of an owner who has provided every facility for a thorough examination of the Natural History in every direction. The vegetation forms well-defined groups, including maritime halophytes and rock-plants, mesophytic grass-land and Bracken, hydrophytic associations, and an interesting rock-desert association of *Sedum anglicum*. The first step in examining the ecology has been the charting of the principal associations, and the results, illustrated by a splendid series of plant-photographs by Mr. R. Welch, were communicated. There is little doubt that Lambay offers exceptional opportunities for ecological observations of great value, and it is probable that the last has not been heard of it.

A further contribution on the Vegetation of Yorkshire was given by Dr. W. G. Smith, who exhibited the field-maps almost completed of North-East Yorkshire from the Tees south to the Vale of Pickering. The district is distinguished by a small number of plant-associations which are uniform over a wide area. A recent investigation on the glaciation of the district enables one to define with much precision the glaciated from the non-glaciated areas, and to see that the vegetation has been influenced by this. A comparison between a varied selection of geological strata and the vegetation shows that plant-distribution is more uniform than geological. The distinguishing plant-formation of the extensive moorlands is *Calluna*-heath on very shallow peat, the occasional occurrence of deeper peat enabling one to see its influence. The district has also proved a good one for investigating the distribution of trees and bracken, which are entirely confined to valleys, valley-slopes and escarpments, so that the upper limit depends on the change from deep-soiled slopes to shallow-soiled plateau, a limit which may vary from 800 to 1,200 feet according to topography. The long extent of coast-line is mainly composed of Boulder Clay or Oolite or Lias Cliffs with grass and scrub and occasionally a coast-wood, while salt-marsh and sand-vegetation is very limited in extent.

Mr. C. E. Moss dealt with the Vegetation of Somerset, briefly explaining the chief features of this memoir, which has since been published by the Royal Geographical Society (see NEW PHYTOLOGIST, February, 1907).

The progress of ecological work at Erquy in 1906 was described by Professor F. W. Oliver. The need for prolonged observations on a limited area has been demonstrated by the exceptional drought of 1906, which has had a remarkable effect on the diminished size and increased numbers of annual species like *Salicornia* and *Suæda*. The results of transplantation of salt-marsh plants from a habitat of one kind to that of another character were also given. The work at Erquy always attracts attention at the Meetings since it is the pioneer effort in a direction which is increasing in importance, and must receive more and more attention from ecologists. (See NEW PHYTOLOGIST, October, 1906). W.G.S.

TWO BOOKS ON THE "PRINCIPLES OF BOTANY."

Principes de Botanique par R. CHODAT, Professeur dé Botanique a l' Université de Genève. Pp. VIII. and 744, avec 829 gravures dans le texte. Genève, 1907.

Principles of Botany by JOSEPH Y. BERGEN and BRADLEY M. DAVIS. Ginn & Co., Boston, etc, 1906.

BOOKS professing to deal with the "principles" of a subject do not always justify their profession, and the reader is apt to be disappointed when he finds that he is confronted with a text-book rather than with a work setting forth the fundamental ideas and conceptions that lie at the root of a department of science. While Messrs. Bergen & Davis are to some extent open to this reproach, the substance of Professor Chodat's book fairly bears out its title. "L' auteur de ce livre," says the Geneva Professor in the first words of his preface "a voulu présenter à tous ceux qui, de près ou de loin, peuvent s' intéresser aux théories de la Botanique un résumé aussi concis que possible des principes généraux de cette branche du savoir humain." He goes on to explain that he has not feared to draw attention to certain problems of physics and chemistry, because a knowledge of these subjects has become absolutely indispensable to biologists worthy of the name. At the same time, says Professor Chodat, this is not the whole of biology. The problem of life is bound up with an actual material which is at present irreducible to simple physical and chemical data, and there are numerous phenomena of morphology and anatomy which must be studied for themselves, and which can be arranged under certain general types. Even the best studied question can be put back into the workshop, and the field for work is just as vast for us as it was for our predecessors.

This will give a sufficient idea of the general aim and scope of Professor Chodat's very original work; we have only space for comment on a very few points. The subject matter is dealt with under four main heads:—General Physiology, the Cell and Tissues, Special Physiology, and Phylogeny. The section on General Physiology contains two chapters, on the constitution of living matter, and on the "captation" and transformation of energy, respectively. A brief account is given of the present state of knowledge on the different branches of these subjects, the general treatment being, as we should expect from the author, specially in relation to modern physico-chemical theory. In discussing carbon-assimilation, the author remarks that no general laws can be established, since individual species have their own peculiarities. It may be objected, however, to this statement that on theoretical grounds we should expect general laws, modified in their working by individual differences of *structure*, whose effects should be determinable. The chapter on anatomy is not the strongest part of the book, and the treatment of some topics, *e.g.*, the transition from root to stem, and the vascular system of ferns, is not at all good, though the idea of giving the "essentials of anatomy" in a short compass should be a perfectly feasible one. The treatment of Special Physiology is novel and interesting, though the classification of "morphoses" and "tactisms" is perhaps too elaborate and rigid. The final section on "Phylogeny" is interesting throughout, and nearly all the recent lines of work on heredity and variation receive some attention.

There are no references in the body of the work—the author remarks that anything like a full bibliography would have occupied fifty pages—but there is a list of the more important general modern treatises arranged under the general heads into which the author divides the subject, and there is also a list of the more important botanical journals. While one may be permitted to doubt whether the non-botanical scientific man could obtain a good idea of modern botany from a work such as this—or indeed from any work of similar length planned on these lines—Professor Chodat's book may be very cordially recommended to the botanist, who will find in it a thoughtful, often original, and sometimes distinctly luminous, succinct exposition of most of the fundamentals of modern botany.

Messrs. Bergen & Davis' book is really a text-book divided into three sections, the first, by Mr. Bergen, being a brief account of the structure and physiology of the flowering plant. The familiar material is well and intelligently treated. Some of the physiology is not quite up to date. For instance the treatment on p. 116 of the conditions of assimilation and respiration require serious revision in the light of Blackman's work on optima and "limiting factors." Dr. Davis' contribution to the book is an evolutionary treatment of the vegetable kingdom from the lowest to the highest forms. This is attractively carried out and should certainly arouse the interest of the student. While much of the section is of a high degree of excellence, exception may be taken to certain passages. Even the doughtiest adherent of the theory of the antithetic origin of the Pteridophytic sporophyte would hardly contend that that theory is certainly established and should be treated as a dogma, yet that is practically how Dr. Davis treats it. The attention devoted to fossils is in the present state of comparative morphology quite inadequate, and the remarks that are made do not properly bring out the importance and real bearing of recent discoveries. The final section on Ecology by Mr. Bergen is most judicious. The author has threaded his way with great skill through the difficulties and ambiguities of this subject and has yet succeeded in bringing out its interest and attractiveness very fully. There are a number of nice new illustrations and a few excellent "half-tones" of vegetation. It is always a little difficult to tell whether a book like this is intended for the teacher or the student, or both. It seems that a teacher who undertakes a course of the range of the subject matter here dealt with should not be content with so brief a treatment, while a student could scarcely acquire a sound knowledge from so condensed a treatise. But this criticism applies to so many text-books that perhaps it is a little otiose. The present work is certainly a favourable example of a modern text-book.

R. MADLEY, Printer, 151, Whitfield Street, Fitzroy Square W.

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DOUBLE NUMBER.

VOL. VI., Nos. 6 & 7. JUNE & JULY, 1907.

[PLATES IV. AND V.]

THE
NEW PHYTOLOGIST

A BRITISH BOTANICAL JOURNAL,

EDITED BY A. G. TANSLEY, M.A., F.L.S.

ASSISTANT PROFESSOR OF BOTANY IN UNIVERSITY COLLEGE, LONDON.

Contents:

LECTURES ON THE EVOLUTION OF THE FILICINEAN VASCULAR SYSTEM.
IV.—THE GLEICHENIACEÆ AND LINDSAYEÆ. [FIGS. 34—46.]
V.—THE EVOLUTION OF THE SOLENOSTELE. THE SCHIZÆACEÆ. [FIGS. 47—50] - - - - - - *A. G. Tansley.*

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THE NATURAL HYBRID BETWEEN THE COWSLIP AND OXLIP. [WITH PLATE V. AND TEXT-FIGS. 5 AND 6.] - - - - - - - - - - *A. W. Hill.*

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ON THE ASSIMILATORY TISSUE OF MANGROVE SEEDLINGS. [TEXT-FIGS. 8—10.] - - - - *M. Carson.*

XEROPHILY AND THE DECIDUOUS HABIT - - *C. E. Moss.*

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CENTRAL COMMITTEE FOR THE SURVEY AND STUDY OF BRITISH VEGETATION.

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NEW PHYTOLOGIST.

VOL. VI., No. 6 & 7. JUNE & JULY, 1907.

LECTURES ON THE EVOLUTION OF THE FILICINEAN VASCULAR SYSTEM.[1]

BY A. G. TANSLEY, M.A.

(Lecturer on Plant Anatomy at University College, London).

LECTURE IV.

THE GLEICHENIACEÆ AND LINDSAYEÆ.

[FIGS. 34—46.]

WE must now consider the Gleicheniaceæ,[2] a family represented by the very characteristic genus, *Gleichenia*. Two of the most aberrant species are sometimes separated as distinct genera— *G. (Platyzoma) microphylla* from North Australia, and *G. (Stromatopteris) moniliformis* from New Caledonia. Both are very xerophilous and distinctly reduced species. Of the two, *Platyzoma* has the more aberrant vascular system. Like the Hymenophyllaceæ, the Gleicheniaceæ are mainly tropical in distribution, but the different species are adapted to a much greater variety of habitat, some being quite xerophilous while others are shade plants. *G. linearis (dichotoma)* is one of the most widely spread and successful of tropical ferns, constantly covering the cleared edges of forests, roadsides, etc., with a thick, almost impenetrable growth of freely branching fronds.

The great characteristic of the fronds is their so-called "dichotomous" branching. The petiole forks into two equivalent branches; each branch may again fork into two, and so on. Pinnæ are borne either by all the branches of the rachis (Sect. *Holopterygium* of Diels) or by the ultimate ones only (*Acropterygium*). A bud is very often borne in the angle of each fork of the rachis, and this bud (especially that of the primary fork) may grow out and form a continuation of the rachis below. These buds are frequently spoken of as "adventitious," but there seems to be no real reason for regarding them as anything but (temporarily) arrested continuations of the rachis. Each bud contains a direct continuation of the primary C-shaped vascular strand of the rachis, and the vascular strands of the primary branches clearly arise from the sides of this. Boodle ('01 B) has pointed out the possibility of deriving an ordinary pinnate fern-frond from the *Gleichenia*-type, the first pair of primary pinnæ of the former being considered as equivalent to the first branches of the latter type of frond; with this view of the homology I should entirely agree. The rhizome (except in *Stromatopteris*) is always creeping and usually subterranean, the leaves being typically inserted at comparatively long intervals.

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[1] A Course of Advanced Lectures in Botany given for the University of London at University College in the Lent Term, 1907.

[2] The substance of the first part of this lecture is largely based on the excellent work of Boodle ('01 B).

The rhizome has a single "solid" vascular cylinder; the tracheæ of the xylem, which fills up the centre of the stele, being interspersed with parenchyma. The position of the spiral protoxylems is characteristic. They are situated just below the surface of the metaxylem at about equal intervals round the periphery of the stele, which is sometimes lobed in relation to the insertion of roots (Fig. 34). This *mesarch* "protostely" is probably secondary in ferns, and may, as we have already seen (p. 117), be derived from the endarch type and be dependent on the relation of the size and shape of the leaf-trace to that of the stele. In the rhizomes of some species spiral protoxylems are quite absent.

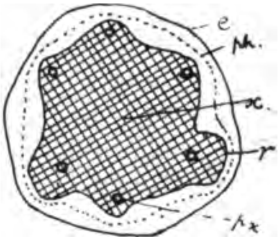

Fig. 34. *Gleichenia linearis.* T. S. of stele of internode. *e.*, endodermis; *ph.*, phloem, indicated by an interrupted line; *x.*, metaxylem, cross-hatched; *px.*, protoxylems indicated by circles; *r.*, root stele attachment. From Boodle.

The conventional indications of phloem, xylem and protoxylem are used in all the following diagrams.

There are two well-marked sub-genera of the more typical Gleichenias—*Mertensia*, which has its pinnules more or less elongated, and *Eugleichenia*, in which the pinnules are small and rounded. The latter sub-genus is to all appearance distinctly more xerophilous than the former. The cross-section of the leaf-trace is distinctive in the two sub-genera. That of *Mertensia* is typically C-shaped as a whole, *i.e.*, the curved band of xylem is covered with a layer of pericycle and endodermis, which follows the curve of the xylem both within and without. The phloem does not line the whole concavity of the xylem arch though it extends round the free ends. This is also the typical form of leaf-trace in solenostelic ferns, though in most cases the phloem completely lines the concavity of the xylem arch. In G. (*Mertensia*) *linearis*, which stands apart from the other Mertensias in more than one respect, the sclerenchyma in the concavity of the petiolar strand is completely enclosed by a separate internal endodermis not continuous with the external one, so that this sclerenchyma is quite shut off from the cortex (Fig. 35). This type of structure is intermediate between the *Mertensia*- and the *Eugleichenia*-types.

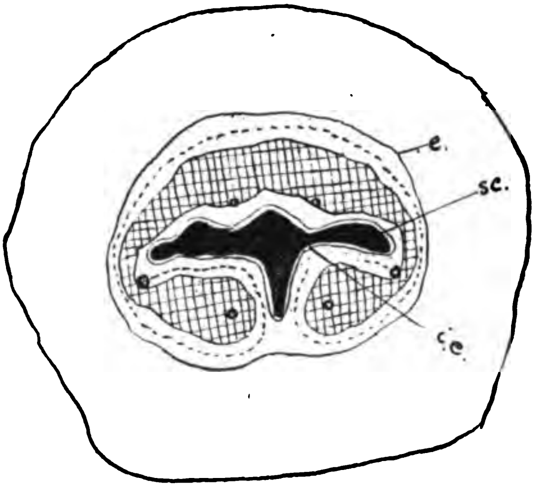

Fig. 35. *Gleichenia linearis*. T. S. of petiolar strand. *e*, external endodermis; *i.e.*, internal endodermis; *sc.*, sclerenchyma. From Boodle.

The petiolar strand of *Eugleichenia* somewhat resembles the commonest Hymenophyllaceous type, *i.e.*, the outline of the endodermis is circular or oval in section, enclosing an arch-shaped. xylem with the free ends terminating in incurved hooks. The phloem however, unlike that of the Hymenophyllaceæ, often passes in round the xylem hooks, and sometimes (*e.g.* in *G. dicarpa*) forms an almost complete lining to the xylem arch (Fig. 36). The central parenchyma of the petiolar bundle sometimes has a strand of sclerenchyma in its midst (Fig. 36), as in *Trichomanes Prieurii*. This is not bounded by an internal endodermis, as in *G. linearis*, but in the base of the petiole an isolated internal endodermis appears in some species (*G. dicarpa* Fig. 37D), *G. circinata* (Fig. 38) enclosing a strand of sclerenchyma within the main sclerenchymatous mass. In *G. dicarpa* this internal endodermis comes into connexion with the external one during the junction of the leaf-trace with the stele of the rhizome (Fig. 37C), thus putting the enclosed strand into open communication with the cortical ground-tissue. Almost immediately, however, the internal endodermis

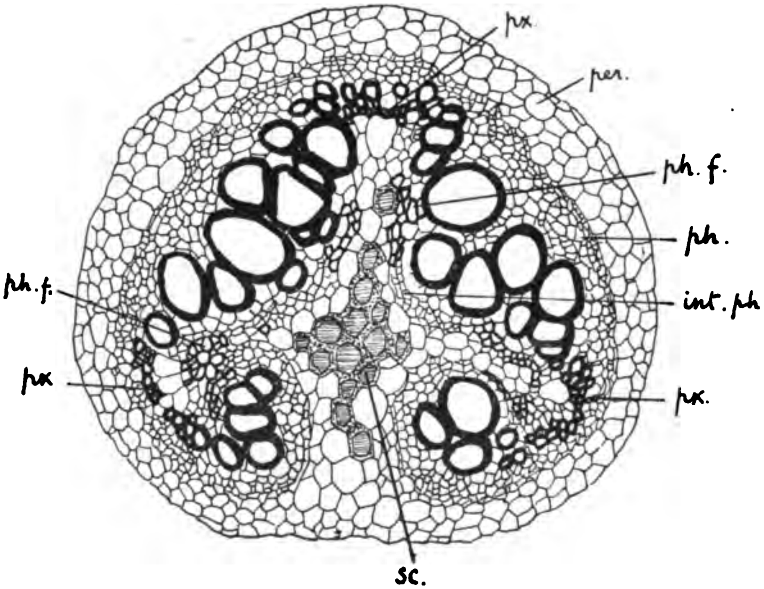

Fig. 36. *Gleichenia dicarpa*. T. S. of petiolar strand. *per.*, pericycle ; *ph.*, external phloem ; *px.*, protoxylem ; *int. ph.*, internal phloem ; *ph. f.*, internal phloem fibres ; *sc.*, internal sclerenchyma. After Boodle.

again (Fig. 37B) separates from the external one, and finally dies out together with the enclosed fibres. In *G circinata* the internal endodermis, with its enclosed fibres, dies out without making any connexion with the cortex (Fig. 38B). In *G. Boryi* there is no sclerenchyma in the concavity of the base of the leaf-trace, but the internal phloem, which in *G. dicarpa* loses itself in the external phloem of the stele during the junction, is continued down, as it is in *G. circinata*, into the xylem of the stele for a short distance, forming a " nodal island " or pocket of phloem which dies out in the xylem.

Turning again to the sub-genus *Mertensia* we find that the leaf-trace of *G. linearis*, which, as we have seen, has a petiolar structure intermediate between that of *Eugleichenia* and that of the typical Mertensias, affects the nodal structure of the rhizome considerably more than is the case in *Eugleichenia*. Though there is a good deal of variation in detail, in none of the cases examined by Boodle does the internal endodermis connect with the external. It is, on the other hand, always continued down with its enclosed

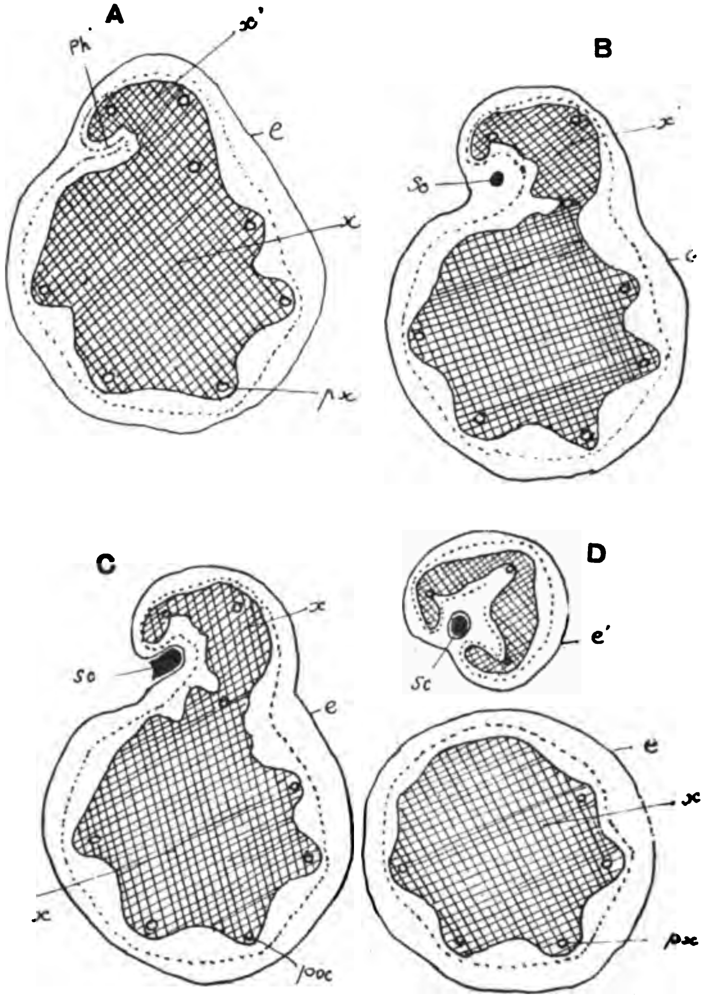

Fig. 37. *Gleichenia dicarpa*. Series of transverse sections through stele of node, showing departure of leaf-trace. From Boodle.

sclerenchyma into the xylem of the stele to form rather a bulky pocket which dies out below the node (Fig. 39). Sometimes a slight branch is also formed penetrating the xylem in an acroscopic direction (Fig. 39 C, D). The internal phloem of the leaf-trace also passes down into the pocket, forming a few sieve tubes on the side of the internal endodermis nearest the centre of the rhizome axis (Fig. 39 B, C, D). Occasionally the internal phloem connects with the external at the insertion of the trace, but usually the leaf-trace joins the stele in the form of a closed ring, and no connexion between the internal and external tissues takes place. In *G. flabellata* (Fig. 40) the internal phloem, the internal endodermis and the sclerenchyma in the concavity of the C-shaped leaf-trace are continued down into the xylem of the stele below the node to form a bulky pocket. The sclerenchyma and endodermis first die out, leaving the internal phloem, which eventually also dwindles and disappears.

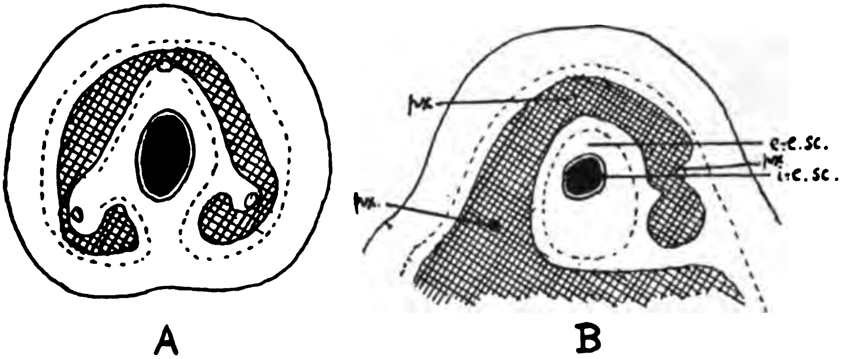

Fig. 38. *Gleichenia circinata.*

A. T. S., leaf-trace.

B. Junction of leaf-trace with stele. *e.-e.sc.*, extra-endodermal sclerenchyma; *i.-e.sc.*, intra-endodermal sclerenchyma.

G. pectinata (Fig. 41) is a solenostelic form, with a normal centrally placed sclerenchymatous pith in the internodes, surrounded by endodermis and internal phloem. A bulky "nodal island" is formed in connexion with the junction of the large C-shaped leaf-trace with the stele. This connects with the pith at the node, but is sometimes, at least, continued for some distance down into the internode in a dorsal position, independently of the pith (Fig. 41C).

Finally, *Platyzoma* has a curious and rare type of stele (Fig. 42), containing a pith surrounded by an endodermis but no internal phloem, and with quite small collateral leaf-traces, whose departure does not break the continuity of the vascular ring as it does in the normal solenostelic type.

It is obvious that the types described fall into a rough series extending from the simpler forms of *Eugleichenia* on the one hand, through the types with internal endodermis at the base of the petiole only, and then through *G. linearis*, to the typical Mertensias and finally to *G. pectinata*. It is scarcely possible, however, to regard this as a progressive evolutionary series, in spite of the fact that the simpler forms have a certain resemblance to many of the

Hymenophyllaceæ, which we have seen some reason to suppose may be regarded as showing comparatively primitive types of Filicinean vascular structure. The isolated or almost isolated internal endodermis of forms like *G. circinata*, *G. dicarpa* and *G. linearis* is difficult to regard as anything but a structure reduced,

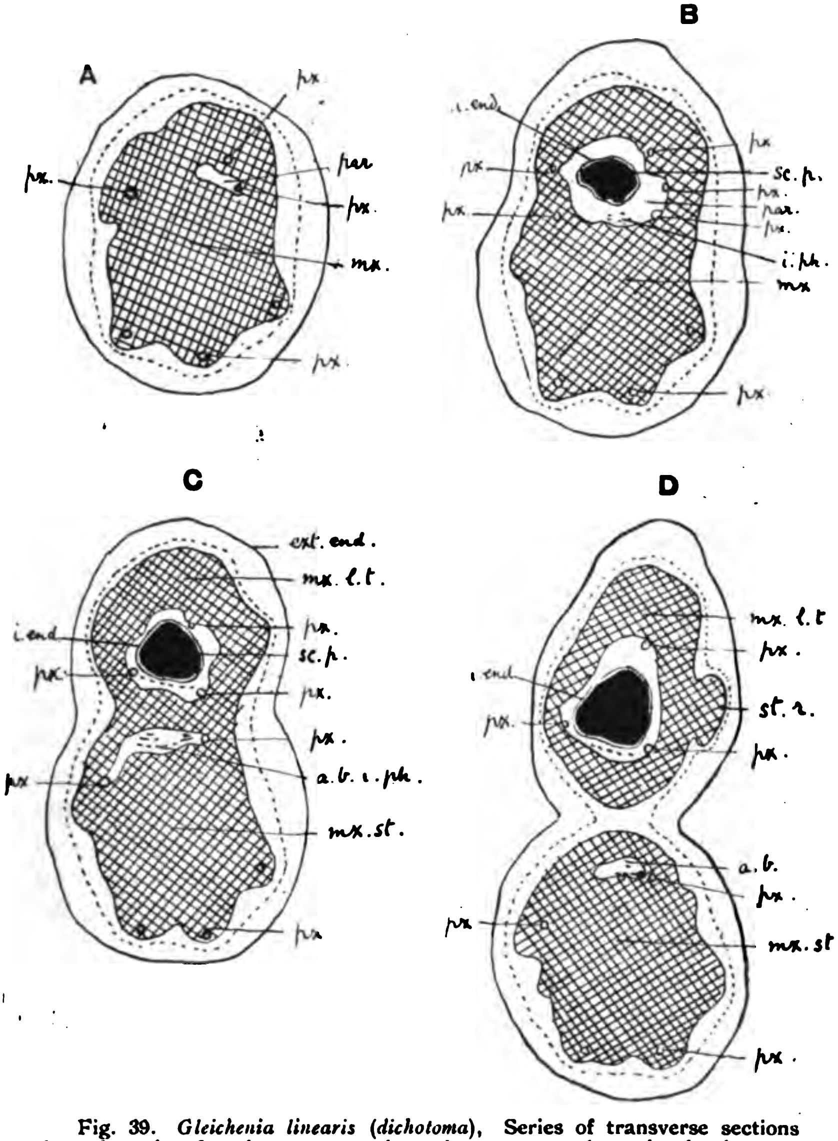

Fig. 39. *Gleichenia linearis* (*dichotoma*), Series of transverse sections through stele of node. *sc. p.*, sclerenchymatous pocket; *i. ph.*, internal phloem, confined to adaxial side of pocket; *a. b. i. ph.*, acroscopic branch of internal phloem; *par.*, parenchyma, forming lower end of pocket; *st. r.*, stele of root arising from base of leaf-trace. From Boodle.

from the form found in the typical Mertensias,[1] for it is impossible to suppose that an isolated endodermis shut up in sclerenchymatous tissue can have an actual function. Further the fact that the Eugleichenias compared with the Mertensias are xerophilous forms distinctly lends support to the theory of reduction as applied to this series.

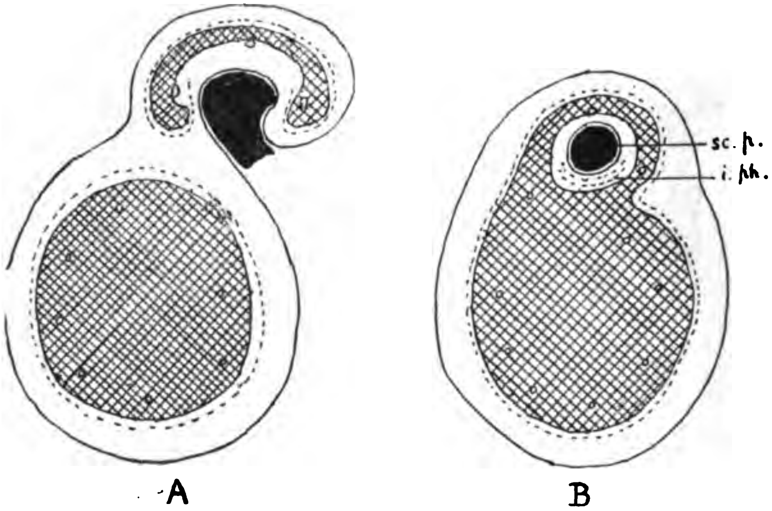

Fig. 40. *Gleichenia flabellata.* Transverse sections through stele of node. *sc. p.*, sclerenchyma of pocket; *i. ph.*, internal phloem.

G. pectinata, on the other hand, is best regarded as derived from the Mertensia-type by the evolution of a regular pith. The co-existence in some cases of the nodal island, or, as it is better called, the nodal pocket, with the ordinary pith in this species is a curious feature scarcely compatible with the derivation of the *Mertensia*-type by reduction from a normal solenostelic form. *Platyzoma* again, with its extreme xerophily and anomalous leaf-traces may almost certainly be regarded as reduced from the solenostelic type.

We are therefore led to the conclusion that such a form as *G. flabellata* on the whole represents the most primitive type of the genus, and it is interesting to note that not only do the branching of the fronds and the form of the pinnules but also the large number of spores in the sporangium (Bower, '99) tend to corroborate this view.

THE LINDSAYA-TYPE.

The next type of Filicinean vascular structure, naturally connecting with the *Mertensia*-type as seen in *Gleichenia flabellata*,

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[1] This view was put forward by Boodle ('01 B).

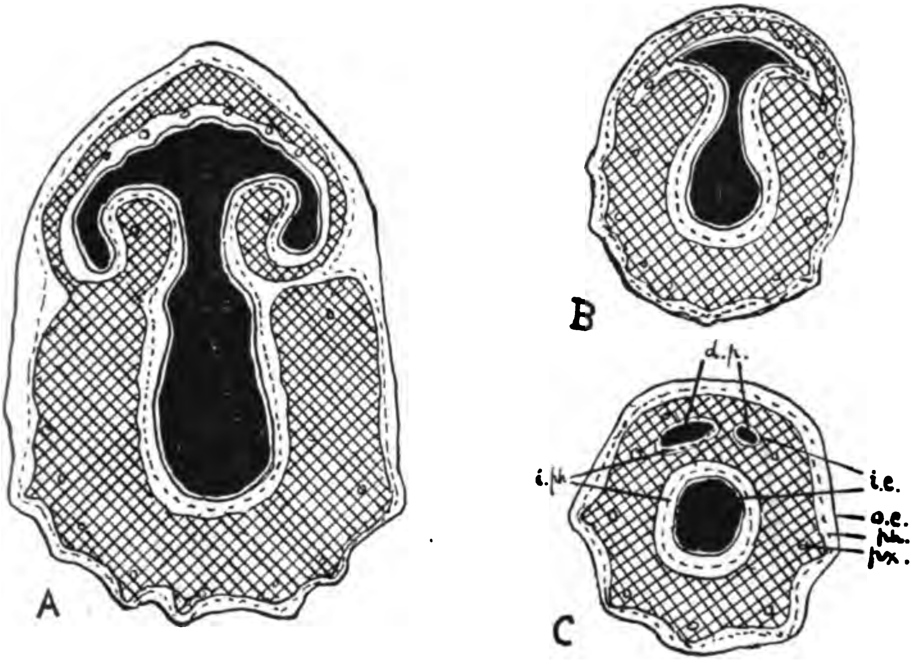

Fig. 41. *Gleichenia pectinata.*

A. Junction of leaf-trace with stele of rhizome.

B. T. S., behind node showing connexion of dorsal pocket with pith still open.

C. T. S., further back, showing dorsal pocket, (*d.p.*) split into two and separate from pith.

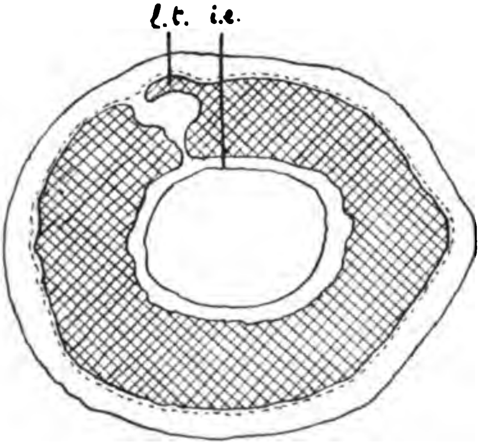

Fig. 42. *Platyzoma microphylla.* Diagram of stele of rhizome showing internal endodermis (*i.e.*,) with pith, but no internal phloem. Only a single leaf-trace (*l.t.*,) is shown leaving the xylem. As a matter of fact the leaves are polystichous, and in any given section a number of traces would be seen. Modified from Boodle.

is the *Lindsaya*-type, characteristic, though not exclusive, in the genus *Lindsaya*, and also found in *Davallia* (*Odontoloma*) *repens*.

Lindsaya is a tropical genus showing a preponderance of shade-forms and with an unmistakably "mixed" sorus; it is usually placed in a separate family Lindsayeæ, closely allied to the Davallieæ, and, by its foliage and the position of its sorus, to Adianteæ also. Gwynne-Vaughan's work ('03) has shown that certain species which are placed by Hooker and Baker (Synopsis Filicum) in the genus *Davallia*, agree closely with the *Lindsaya*-type of anatomy, and since these species have all been put, at various times, by one authority or another, in separate genera, and their general characters also sufficiently agree with *Lindsaya*, we seem fully justified in associating them under separate generic names in the family of Lindsayeæ.

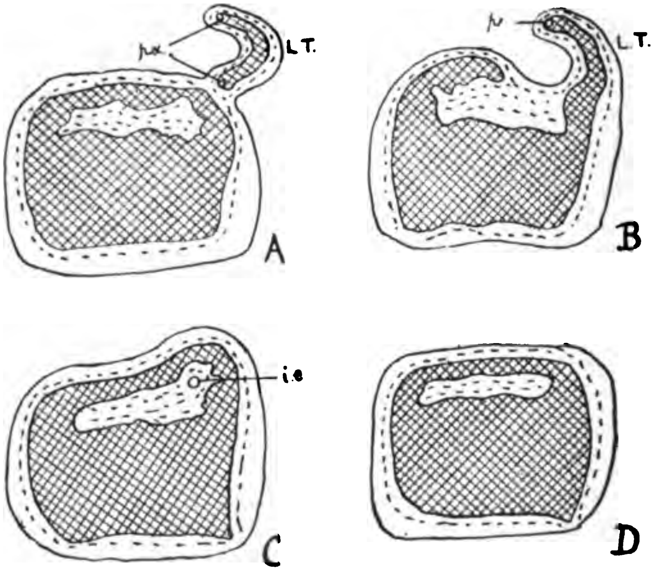

Fig. 43. *Lindsaya scandens.* Series through node, showing internal phloem and mode of attachment of leaf-trace.

The internode of a typical *Lindsaya* (Tansley and Lulham '02) shows a dorsiventral stele with mainly "solid" xylem, but with an internal strand of phloem running close to its dorsal surface (Fig. 43D). The xylem has a good deal of intermixed parenchyma, as in *Gleichenia*, but no spiral protoxylem.

The petiolar strand is "subrotund or cordate" in cross section, the xylem consisting of two more or less distinct arms inclined to one another at an acute angle, approaching to a right angle, which is of course directed away from the stem-axis (Fig. 44). "The protoxylem groups are distinct and endarch; one occurs at the end of each arm of the xylem, and sometimes a third is also present at its apex. The arms of the xylem-strand are sometimes prolonged past the two lateral protoxylems, curving inwards towards the plane of symmetry of the petiole so as to form two small hooks. These hooks are included in the phloem of the bundle, which is perfectly continuous all round the xylem-strand" (Gwynne-Vaughan, '03). The leaf-trace leaves the stele by the breaking of the dorsal arch of xylem which covers the internal phloem, and the passing off of tracheids, together with surrounding tissue, from one side of the arch, which soon re-closes. The internal phloem of the stele is therefore continuous with that of the trace, and the whole structure is essentially what would result if the nodal pocket of phloem in *Gleichenia* were continued down through the internode to join that of the node below. Owing to the somewhat different shape of the leaf-trace the concavity is much less marked, and the ground tissue surrounded by endodermis is not carried down so far into the stele as is the case in *Gleichenia flabellata*, but in some cases there is a short endodermal pocket extending into the internal phloem below the node (Fig. 43 C).

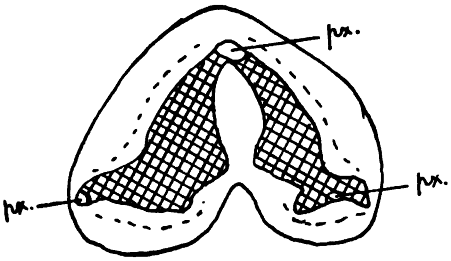

Fig. 44. *Odontoloma repens.* T. S. of petiolar strand. After Gwynne-Vaughan.

The *Lindsaya*-type of stele is found in all the species which have been examined of *Davallia* §*Odontoloma* and §*Stenoloma* (Synopsis Filicum) except *Davallia* (*Stenoloma*) *aculeata* (see Gwynne-Vaughan, '03). This last named species, which has been put in a separate genus *Lindsayopsis* by Christ, and *Davallia pinnata*, which has been separated as *Wibelia* by Christ, show a further modification of the *Lindsaya*-type.

Wibelia pinnata (Fig. 45) has a strand of sclerenchyma in the concavity of the leaf-trace (Fig. 45 A) and this is continued down

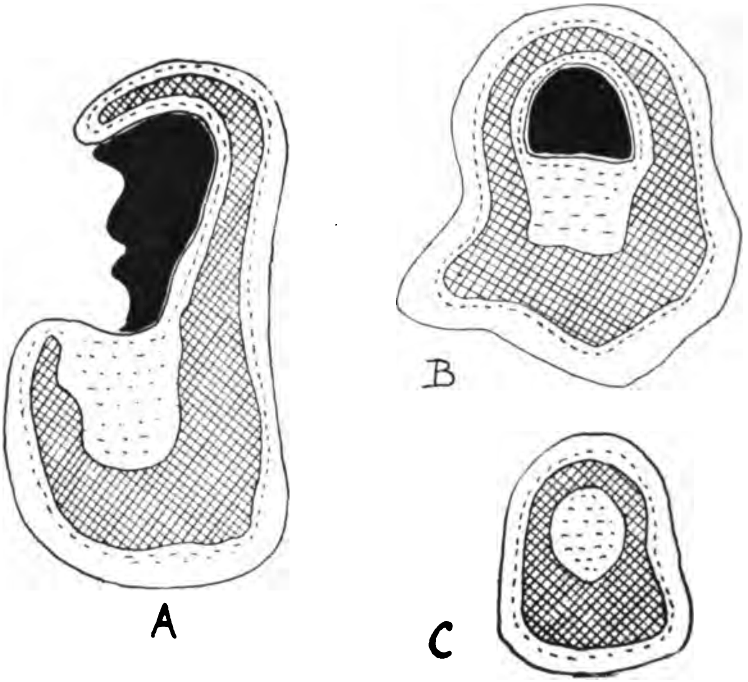

Fig. 45. *Wibelia pinnata.*

A. T. S. of stele at node showing attachment of leaf-trace with strand of sclerenchyma in its concavity.

B. T. S. of stele just below node, with internal sclerenchyma and endodermis.

C. T. S. of stele above node.

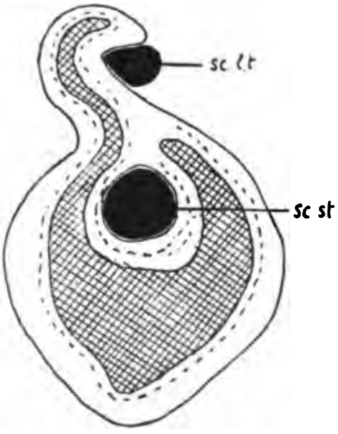

Fig. 46. *Lindsayopsis aculeata.* T. S. of stele of node; *sc. l.t.*, sclerenchyma of leaf-trace concavity; *sc. st.*, sclerenchymatous pith of stele.

as a fairly bulky strand surrounded by an endodermis into the internal phloem of the stele (Fig. 45 B). It is persistent through most of the internode but gradually dwindles and disappears before the next node below is reached. A transverse section just above the node therefore shows the pure *Lindsaya*-type (Fig. 45 C).

In *Lindsayopsis aculeata* (Fig. 46) the internal sclerenchyma reaches the next node and joins the incoming strand belonging to that leaf-trace, so that a regular solenostele is formed. This differs however from a perfectly typical solenostele, owing to the fact that the xylem on the ventral side of the internal phloem is considerably thicker than the dorsal arch of xylem; though this difference is not so extreme as in certain species of *Lindsaya* and *Odontoloma*. Finally in two species of *Lindsaya*, *L. cultrata* and *L. retusa*, a typical solenostele is present.

LECTURE V.

THE EVOLUTION OF THE SOLENOSTELE.—THE SCHIZÆACEÆ.

[FIGS. 47—50.]

THE series of types described in the last lecture clearly forms a beautifully complete chain connecting the protostele with the solenostele, and there is the strongest reason to believe that the latter type of vascular structure has arisen from the former through similar phylogenetic stages, though it is quite possible that the solenostele or some similar type of structure may in other cases have arisen somewhat differently. It may of course be suggested that the *Wibelia*- and *Lindsaya*-types are derived by reduction from the solenostelic condition. There is however nothing whatever to suggest such reduction, and in Gwynne-Vaughan's opinion ('03, p. 718), "the increased thickness of the lower region of the xylem-ring forms an insuperable objection to the general application of any reduction hypothesis to this series." As this author points out ('03 p. 717), "if such a series of changes" [as would be brought about by the gradual extension first of the phloem, and then of the sclerenchymatous ground tissue, or by both of these simultaneously, from the concavity of the leaf-trace into the xylem of the stele, till connexions were formed with the same tissues from the next leaf-trace below] "were to take place in a dorsiventral rhizome with the leaves inserted only on the dorsal surface, it is extremely probable that the phloem and ground tissue decurrent from the leaf-traces would not at first occupy the very centre of the stele, but would lie nearest to the dorsal surface on which the leaves are inserted, and hence the ventral portion of the xylem-ring would be broader than the dorsal, as is actually the case " in these types.

Another objection which may be urged against the belief that the stelar types characteristic of the Lindsayeæ are immediately derived from those found among the Gleichenias, is the fact that while the latter belong to the lowest soral grade—the Simplices, the former are typical Mixtæ. It is however perfectly possible to suppose that in some cases the evolution of a " mixed " type of sorus took place with comparative rapidity from a primitive condition, while the stelar system was relatively little modified, and this interpretation is strengthened by the fact that transitions from one type of sorus to another are known within the limits of a single genus in more than one instance.

The evolutionary series indicated is also very strongly supported by evidence from the anatomy of the young plants of the more advanced Leptosporangiate ferns, a topic with which it will be more convenient to deal separately in a later lecture.

FACTORS IN THE EVOLUTION OF SOLENOSTELY.

Having thus traced the evolution of the solenostele from the protostele through a very complete series of intermediate forms, it remains to enquire as to the factors which have brought about such a course of evolution.

The first point we have to notice is that the solenostele is normally associated with the arched type of leaf-trace, *i.e.* with a type which itself resembles a solenostele incomplete on one side. It is a striking fact that this type of leaf-trace is also found in many protostelic forms. We saw in the second lecture that the C-shaped type of petiolar strand is common in the protostelic Botryopterideæ though the leaf-trace itself is isodiametric or nearly so. We also saw that there is a very widespread if not a universal tendency to what I have called " basipetal evolution " of the vascular system, based no doubt on the fact that the evolution of the leaf itself is the main determining factor in the changes occurring in the vegetative body. The C-shaped type of petiolar strand is correlated with a flat frond possessing lateral pinnæ, and whatever the exact method of origin it is certainly well adapted to the vascular supply of such a frond. Increased demands on the part of the leaf will certainly tend to the carrying down of the C-shaped structure to the point of junction of the stele of the rhizome, and this is the condition found in such a form as *Gleichenia flabellata*. The effect of the insertion of a broad C-shaped trace upon a protostele is not difficult to understand. The current of water passing up the rhizome and partly deflected into the trace will take a peripheral course and the tracheal elements of the stele opposite the middle of the trace will tend to be depleted of water and eventually cease to be developed. Thus the tissue in the concavity of the trace will tend to be decurrent into the stele, and the "pocket" seen in *Gleichenia* will be developed. At the same time any broadening of the span of the leaf-trace arch will tend to necessitate an increase in the diameter of the stele in order to provide for its insertion. If the xylem of the stele remained solid it would increase as the square of the diameter of the enlarged stele, but this would be in excess of the additional demand, and would again lead to the replacement of the central tracheæ of the stele by passive tissue, and still further to localise peripherally the xylem of the stele. If the central passive tissue is continued down through the internode and joins the decurrent strand of the node below we have a hollow stele developed[1]. Thus the evolution of the solenostele seems to depend primarily on basipetal evolution from the point of insertion of a C-shaped leaf-trace.

Another factor may come into play in the development of a pith consisting of sclerenchyma. The insertion of a solid rod of resistent sclerenchyma in the node, one end of which supports the leaf-trace, while the other runs down the stele of the stem, must tend to strengthen mechanically the junction of the two, which will be a point of weakness in the continuity of the tracheal channels. Though this junction certainly seems to be quite adequately protected by the continuous external plate armour of cortical sclerenchyma in most of the existing types, the internal sclerenchyma will add to the rigidity of the whole system.

The existence of the *Lindsaya*-type not only in the adult Lindsayeæ, but also in the ontogeny of most of the more advanced Fern-stems that have been investigated, shows that the decurrency of internal phloem often precedes the decurrency of internal endodermis and sclerenchyma. It is easy to see that the evolution of a larger leaf-trace in order to supply a more complex frond will involve a demand for an increased conduction of formed food-material away from the frond *pari passu* with increased water conduction. Internal phloem thus developed in the concavity of the leaf-trace, at first by extension round the ends of the C, would not find adequate attachment in the external phloem of the rhizome stele, and an internal strand of phloem in the rhizome might arise by the decurrency of the internal phloem of the trace into the xylem of the stele. But here a difficulty arises, for while it is, as we have seen, quite easy to understand the *rationale* of origin of blind ground-tissue pockets, the function of a blind phloem pocket, such as we find in *Gleichenia flabellata* and other species, is not so intelligible. We know far too little about the actual function of the phloem of ferns to dogmatise on this subject. We certainly cannot be sure that a discontinuous series of phloem pockets has no function. They may act as storage reservoirs, they may feed the developing xylem, but till we know more it is useless to discuss the matter further. Nevertheless, on purely morphological grounds there certainly seems every likelihood that the establishment of phloem pockets in a protostelic type formed the point of departure for the evolution of the *Lindsaya*-type, just as the formation of ground-tissue pockets within the internal phloem formed the point of departure for the evolution of the solenostele.

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[1] The explanation here given is substantially the same as that suggested by Boodle ('01 A).

The formation of a "leaf-gap" in the stele is a necessary consequence of the great dilation of the stele, and the concomitant thinning of the vascular ring, involved in the formation of a solenostele. The vascular ring is "broken" by the departure of the trace, or in other words the vascular elements in the "axil" of the trace, are not developed, owing to the deflection of the water-current on that side of the stele into the tracheæ of the trace itself. The gap so formed in the wall of the stele is "repaired" or "closed," in the typical case, by the development of vascular elements, completing the solenostelic ring, at a higher level, above the area affected by the departure of the trace; in many cases, however, particularly where the vascular ring has a large diameter, the closing of the gap is effected in another way, as we shall see in a future lecture. The gap may be confined to the base of the leaf-trace or it may extend for some little distance forward along the rhizome-stele. A few solenostelic ferns have no leaf gaps, but this is pretty certainly always due to reduction of the trace in relation to the stele so that a smaller relative demand is made upon the latter for the supply of any given leaf. In the *Lindsaya*-type a gap is usually made in the dorsal arch of xylem covering the internal phloem. It is, in most cases, of small size and quickly repaired, but this depends upon the size of the leaf-trace in relation to the stele.

A solenostele has been defined by Gwynne-Vaughan ('01) as "a single hollow cylinder with phloem and phloeoterma (endodermis and pericycle) on either side, the complete continuity of which is interrupted only by the departure of the leaf-traces; the gaps thus produced being closed up in the internode above before the departure of the next leaf-trace." Sometimes the concavity of the trace faces towards the apex of the rhizome (*Loxsoma*), but more often it faces inwards, *i.e.*, towards the dorsiventral plane (*Hypolepis*, etc., and *Wibelia*, *Lindsayopsis*).

The typical or slightly modified solenostele is rather characteristic of ferns belonging to the middle grades of evolution, though it also occurs in several of the lower and a few of the higher types. In the case of several solenostelic ferns belonging to the Mixtæ, there is some evidence that they represent relatively primitive types of their groups (Gwynne-Vaughan, '03).

THE SCHIZÆACEÆ.

Before passing on to consider the modifications of the solenostele and the evolution of dictyostely, we must devote a short time to the Schizæaceæ, a remarkable family, in some ways primitive, and showing a wide range of vascular structure and some distinct peculiarities.

Of the four genera, the most primitive, *Lygodium*, is characterised by climbing fronds, often of great length, and with the same general construction as those of *Gleichenia*. The stele of the rhizome shows practically the same structure as that of *Trichomanes scandens* (Fig. 29), except for the fact that its peripheral protoxylem elements are scalariform and not spiral, a fact correlated, no doubt, with the slowness of growth of its rhizome. It may probably be regarded as quite a primitive type.

The petiolar strand of *Lygodium* is peculiar, and indeed unique among living ferns. The whole strand is roundish or oval in section. The distribution of xylem and phloem in *L. dichotomum* and *L. japonicum* may best be made clear by means of a diagram (Fig. 47.) cf. *Schizæa elegans* (Fig. 48). The petiolar strands of different species have a general resemblance. In some cases the xylem is more rounded in section than in the species figured, and in *L. palmatum* it has the form of an equilateral triangle with a protoxylem at each angle, the one situated on the abaxial side being distinctly sunk in the metaxylem. Towards the base of the petiole the outline of the xylem in *L. dichotomum* becomes more rounded, the spiral elements of the two lateral protoxylems disappear, and finally the prominence on the lower side becomes narrower, the two spiral protoxylem-strands being replaced by a single strand of narrow scalariform elements which are probably continuous with the peripheral protoxylem of the stele. The phloem, which in the petiole is continuous round the whole strand, with large metaphloem elements localised between the angles, is evenly distributed round the xylem at the base of the leaf-trace. It is not quite easy to explain this peculiar type of petiolar strand, but I am certainly inclined to regard the rounded form of the xylem and the continuous phloem, both characters especially marked at the base of the leaf-trace, as a primitive character, just as I regard the somewhat similar structure of the base of the leaf-trace in *Trichomanes radicans* in the same light. It may here be noted that the leaves of some species of *Lygodium*, though constructed on the same general plan as those of *Gleichenia*, show more tendency to true dichotomy in their branching and in the lobing and venation of their laminæ.

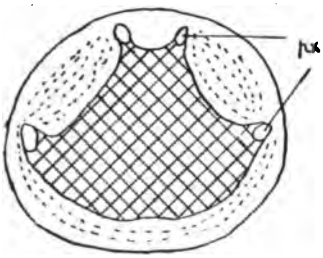

Fig. 47.

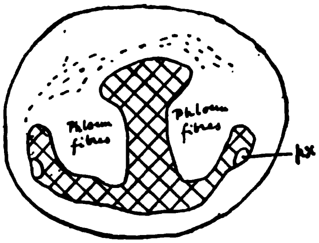

Fig. 48.

Fig. 47. *Lygodium japonicum.* T. S. of petiolar strand. After Prantl.
Fig. 48. *Schizæa elegans.* T. S. of petiolar strand. After Prantl.

The genus *Schizæa* consists of small ferns, mostly characteristic of shady forests, and largely tropical. The fronds of many species are truly dichotomous. The stele of the rhizome is of peculiar type. The thin ring of xylem surrounded by phloem, pericycle and endodermis, encloses a parenchymatous pith which does not, as in most ferns, resemble the cortex histologically, but is usually thin-walled, like xylem-parenchyma; in *S. digitata* it is sclerotic, though even here it differs from the sclerotic cortex. In some species also it contains, locally, tracheids mixed with the parenchyma, occasionally so many that the stele is, at certain levels, little removed from a protostele of the *Lygodium*-type. There seems in fact little doubt that the stele of *Schizæa* is derived from such a protostele, most of the central tracheids being replaced by parenchyma in relation to a reduction in the need for water conduction brought about by the diminished transpiration due to the shade-habit. A similar cause probably led to the development of the somewhat similar pith in most Hymenophyllaceæ. A further complication exists. In at least two species, *S. digitata* and *S. malaccana*, there is a local development of internal endodermal strands, sometimes consisting entirely of endodermal cells, and sometimes enclosing a file of cells with the characters of ground tissue and quite distinct from the surrounding pith. These structures are usually, though not always, decurrent from the leaf-gaps, where they are continuous with the outer endodermis and cortex, thus forming pockets in exactly the same way as in *Gleichenia*, etc. (Fig. 49). Whether the pouches are to be regarded as reduced structures, which they certainly suggest, is rather a difficult question (Boodle '03, Tansley & Lulham '03) that would take us too far to discuss here. In any case there is no evidence of internal phloem having ever existed in the ancestors of *Schizæa* and we must regard this peculiar form of stele as closely related to the *Lygodium*-type. The petiolar bundle of *Schizæa* is collateral and usually band-shaped. That of *S. elegans* (Fig. 48) has a certain resemblance in form to the typical *Lygodium* petiolar strand. The genus *Aneimia* is partly solenostelic, but some of the species, at least, show signs of reduction, and even suggest the *Schizæa*-type, though they have not only a regular internal endodermis, but also internal phloem.

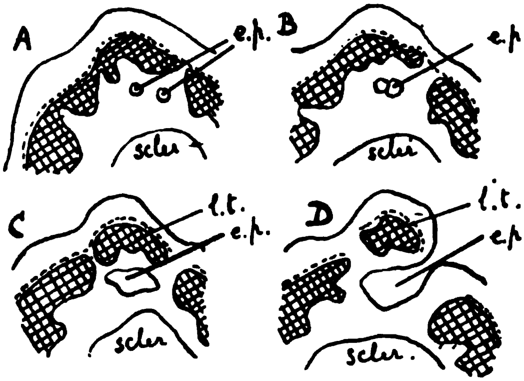

Fig. 49. *Schizæa digitata*. Series of transverse sections of part of the stele from below upwards, showing departure of leaf-trace and endodermal pocket. *e.p.*, endodermal pocket ; *l.t.* leaf-trace ; *scler.*, sclerenchymatous pith. After Boodle.

Aneimia Phyllitidis (Fig. 50) has a simple radial dictyostele which shows very clearly how over-lapping of the leaf-gaps gives rise, as we shall see in the next lecture, to dictyostely. *Mohria* is similar.

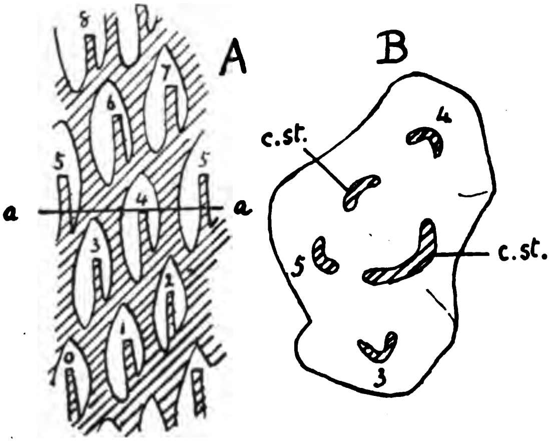

Fig. 50. *Aneimia Phyllitidis.*

A. Diagram of stele seen from side spread out in surface view. The numbers represent successive leaf-traces and gaps.

B. T. S. of stem along the line *a—a* ; *c.st.*, cauline strands. From Prantl.

Thus in this single family of comparatively few genera and relatively primitive status, we have most of the main types of Filicinean stelar system represented, but associated with some interesting and rather anomalous peculiarities.

FERTILIZATION IN *ASCOBOLUS FURFURACEUS*, PERS.,

BY

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[With Plate IV.]

THE study of development among the Ascobolaceæ began in 1866 when Woronin (13) gave a brief description of *Ascophanus pulcherrimus* Cr. (Ascobolus pulcherrimus Cr.) He describes the archicarp as a row of swollen cells which he terms a scolecite. It becomes enclosed in a sheath of mycelial branches, some of which Woronin regards as probably antheridial. In 1871, Janczewski (12) published a somewhat similar account of *Ascobolus furfuraceus*, Pers.; here also the scolecite arises as a curved multicellular branch, and becomes surrounded, as development proceeds, by a dense sheath. As in *Ascophanus pulcherrimus*, the earliest branches of the envelope are supposed to be antheridial. One of the cells near the apex of the scolecite increases in size and gives rise to branches upon which asci are eventually borne. The spores were also germinated, but only after they had been passed through the alimentary canal of an animal. In 1896, Harper (8) published a fuller account of this species. He described the young scolecite as consisting of a row of uninuclear cells connected by large pores, and surrounded by a sheath. The cells of the scolecite become multinuclear, one of them increases in size, and into it nuclei from the other cells migrate through the pores. From the large cell branches arise as described by Janczewski, and into them the nuclei pass.

Dangeard (6) however in 1904 stated that the scolecite, even in the young stages before the sheath is formed, is multinucleate. The pores described by Harper he regards as evidence of protoplasmic connections similar to those found in the vegetative hyphæ. He asserts that the nuclei do not pass through them, but degenerate *in situ*, except in the case of that cell which eventually gives rise to the ascogenous hyphæ.

In 1905, Claussen (5) investigated a species of *Boudiera* in which he found that the young archicarp consists of a stalk, fertile cell and trichogyne, and that after fertilization the ascogonium becomes multicellular, and gives rise to ascogenous hyphæ. Previous to this investigation no cytological evidence of a sexual process had been obtained in the members of this group.

In 1906, Blackman and Fraser (2) described a process of reduced fertilization in *Humaria granulata*; in this form an antheridium is not found and the female nuclei fuse in pairs on the ascogonium. The authors suggest that a similar parthenogenetic fusion probably exists in such other forms as *Ascobolus* where an archicarp but no antheridium had been reported.

A further investigation of *Ascobolus furfuraceus*, Pers, seemed therefore desirable, and was undertaken in the autumn of 1905, abundant material being obtained on cow dung.

Two well-marked colour varieties were found, but they graded into each other, and were therefore used indiscriminately. No definite relation between the colour of the ascocarp and the nature of the substratum could be made out.

Methods.

All stages except the youngest were readily obtained on the natural substratum and such material was therefore employed throughout the research.

Attempts were also made to obtain cultures on agar, but these proved unsuccessful and were ultimately abandoned. Material was collected at various times of the day, but was found to be most satisfactory when fixed about noon.

Various fixing agents were used, but the best results were obtained with Flemming's weaker fluid. Material was embedded through either chloroform or cedar oil. Sections were usually cut 5μ in thickness, and were stained either with Flemming's triple stain or with Heidenhain's iron haematoxylin and a solution of eosin in clove oil (Fraser (7).

ACTUAL OBSERVATIONS.

Mycelium and Chlamydospores.

The cells of the vegetative mycelium are usually multinucleate, rich in protoplasm and as Harper (8) has observed characterised by the presence of granules on their transverse walls.

Chlamydospores closely resembling those figured by Woronin (13) for *Ascophanus pulcherrimus* were frequently observed.

Germination of Ascospores.

The ripe ascospores are ejected in large numbers at about mid-day, and may be readily collected on a cover slip arranged above the ascocarp. After exposure for about twenty-four hours, in watery extract of cow dung, to a temperature of 38°c. that of the body of a cow, the spores germinated. The dung extract was either used alone, or was preceded by treatment with the various digestive fluids. It was also found possible to obtain germination in a centinormal solution of sodium carbonate, but in this case the germ tubes were badly developed, probably owing to the lack of food material. The methods used are fully described by Fraser (7) for *Lachnea stercorea* in which similar results were obtained.

The Development of the Ascocarp.

The ascocarp, in its earliest stages, shows a scolecite of from six to ten usually similar cells arising from a dense tangle of mycelial hyphæ. As a rule the scolecite soon becomes very much curved over, and a differentiation of the cells takes place, those towards the middle of the branch becoming considerably larger than the rest, and the whole structure at the same time rapidly covered by a sheath of branched hyphæ. In section the cells of the young scolecite are seen to be rich in protoplasm, and to contain each a single large nucleus. This stage was rarely found, and probably lasts only a short time, the cells soon becoming multinucleate; figure 3 shows a young scolecite in which the nuclei have already begun to divide, and in figure 4 each cell contains several nuclei. As the cells become multinucleate they increase in size and the ascocarp is seen to consist of a many layered sheath, surrounding the archicarp, of which one cell, generally the fourth from the apex, is larger than the rest and shows small outgrowths which eventually develop as the ascogenous hyphæ. This is therefore the ascogenous cell and corresponds morphologically to the ascogonium of such forms as *Humaria granulata.* The transverse walls of the scolecite are perforated medianly by large circular pores; these are shown in figures 5 and 6, that in figure 6 measuring 5μ in diameter. Pores could not be identified in the earliest stages of development and it seems possible they may be of secondary formation. The nuclei with the cytoplasm of the several cells pass through the pores till they reach the ascogenous cell, where they fuse in pairs (figures 7, 8, 9). The fusion nuclei pass into the ascogenous hyphæ (figure 10) and the ascogonium becomes emptied of its contents, though a little vacuolate cytoplasm with scattered nuclei remains for a time. The empty scolecite eventually collapses. The ascogenous hyphæ develop rapidly, their apices bend over, a terminal and a penultimate cell are cut off and the two nuclei in the latter fuse to form the definitive nucleus of the ascus from which the spore nuclei are derived.

The development of the ascus was not studied in detail, as it has already been fully described by Harper (8).

GENERAL CONCLUSIONS.

Among Ascomycetes the union of the pronuclei in fertilization was first observed by Harper (10) in 1896 for *Sphaerotheca humuli*. The sexual organs are here uninucleate and the fertilized oogonium gives rise to a row of cells. These with the exception of the penultimate binucleate cell, are uninucleate; they are regarded by Harper as an "ascogonium," but by Blackman and Fraser (3) as a single ascogenous hypha.

A similar fertilization occurs in *Erysiphe communis*, Harper (8) and in *Phyllactinia Corylea*, Harper (11). The oogonium in these species gives rise to a row of cells, but here several ascogenous hyphae grow out from the penultimate cell and, in *Phyllactinia* at least, may arise from the other cells also.

In *Pyronema confluens* (9) the male and female cells are coenocytic and fusion between a very large number of nuclei takes place in the ascogonium which without further development branches freely to form the ascogenous hyphae.

Among parthenogenetic forms, a reduced fertilization has been observed in *Humaria granulata*, and *Lachnea stercorea*. In *Lachnea stercorea*, Fraser (7) a trichogyne and antheridium are present but not functional; fusion takes place between the nuclei of the ascogonium.

Humaria granulata, Blackman and Fraser (2), probably shows a further stage of reduction since a trichogyne and antheridium are not developed.

In view of the above facts it seems obvious that the nuclear fusions occurring in the ascogenous cell of *Ascobolus furfuraceus* constitute a reduced sexual process. Here, as in *Humaria granulata*, an antheridium is not present. Though no definite knowledge could be obtained of the relationship of the fusing nuclei or indeed as to whether they necessarily came from the different cells of the scolecite, yet it seems probable that they are more distantly related than are those which fuse in the one-celled ascogonium of *Humaria granulata.* The nuclei which fuse in the ascogenous cell are partly derived from the neighbouring cells of the scolecite. If these cells be regarded as female, the fusions in *Ascobolus furfuraceus* are quite comparable to those seen *Humaria granulata* and *Lachnea stercorea* or to the association of female nuclei in pairs first observed by Christman (4) in *Phragmidium speciosum.* If however the cells of the scolecite be vegetative, the fusions in *Ascobolus furfuraceus* are to be related, rather, to the fertilization of a female by a vegetative nucleus which occurs in *Phragmidium violaceum*, Blackman (1).

I have to thank Miss H. C. I. Fraser, at whose suggestion this work was undertaken, for valuable help and criticism throughout its progress.

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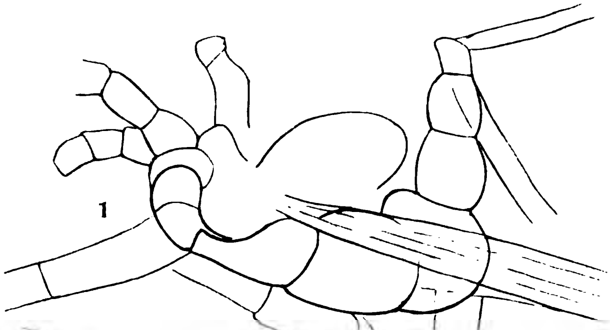
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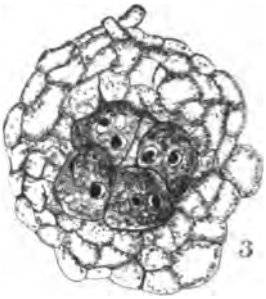
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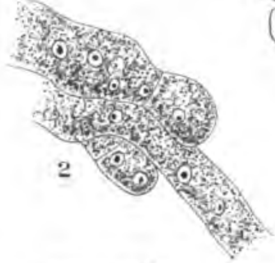
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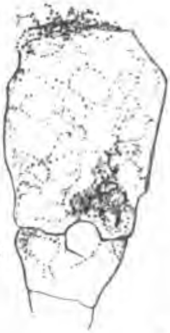
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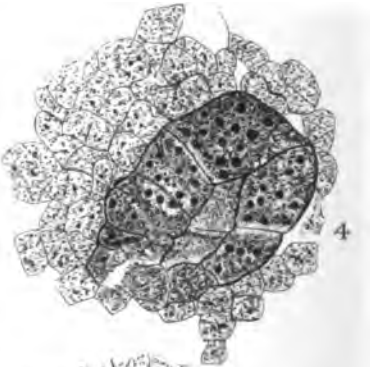
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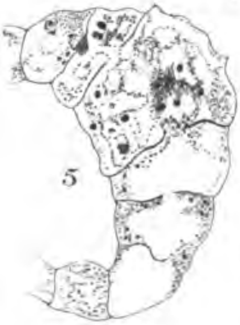
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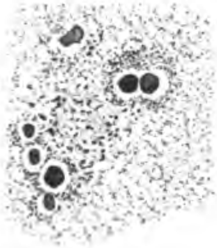
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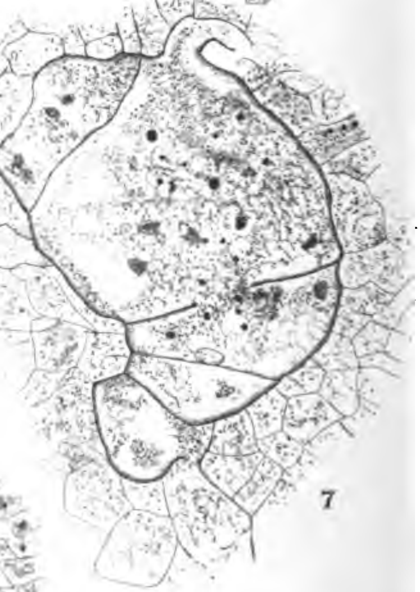
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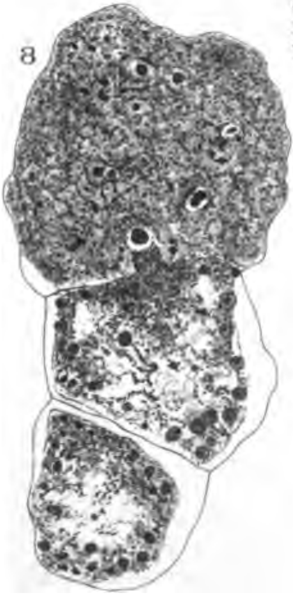
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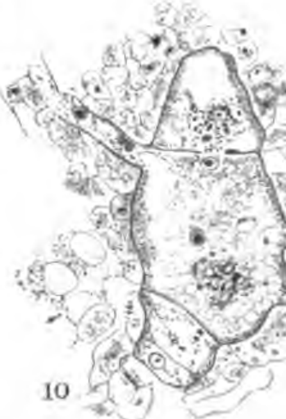
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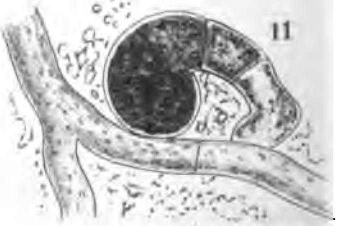
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DESCRIPTION OF FIGURES ON PLATE IV. ILLUSTRATING MISS E. J. WELSFORD'S PAPER ON "FERTILISATION IN *ASCOBOLUS FURFURACEUS*.

Fig. 1. Young Ascocarp. From fresh material. (x 1500).

Fig. 2. Mycelial hyphae showing numerous nuclei. (x 1250).

Fig. 3. Transverse section of a young ascocarp in which the cells of the scolecite are binucleate. (x 625).

Fig. 4. Transverse section of a slightly older asocarp. Numerous nuclei visible in the cells of the scolecite. (x 625).

Fig. 5. Longitudinal section of a scolecite showing passage of cytoplasm through the pores. (x 625).

Fig. 6. Oblique section of scolecite showing pore. (x 625.)

Fig. 7. Scolecite showing migration of nuclei and cytoplasm. (x 1250).

Fig. 8. Longitudinal section of scolecite showing nuclear fusion in ascogenous cell. Nuclei shown in which fusion is complete and others in which the two nucleoli are still separate. (x 1250).

Fig. 9. A single fusion nucleus and another in which the nucleoli have not fused. (x 1250).

Fig. 10. Longitudinal section of scolecite, fusion nucleus in an ascogenous hyphae. (x 625).

Fig. 11. A chlamydospore. From fresh material. (x 625).

THE NATURAL HYBRID BETWEEN THE COWSLIP AND OXLIP,

By Arthur W. Hill, M.A.

[With Plate V. and Text-Figs. 5 and 6.]

ONE of the most interesting features of the flora of the country around Cambridge is the occurrence of the true Oxlip, *Primula elatior* L.—Jacquin's or the Bardfield Oxlip—in certain areas of woodland on the boulder clay, and the absence of the Primrose *P. acaulis* L. from such woods as are well within the Oxlip area.

The exact distribution of the Oxlip has been so beautifully worked out by Miller Christy[1] that it would be superfluous to enter into the question in any further detail in this brief note. Suffice it to say that the main Oxlip area occupies an irregular tract of country on the borders of Cambridgeshire, Essex and Suffolk, with large extensions into Suffolk and Essex; whilst there is a small triangular area to the west of Cambridge, roughly bisected by the old North Road. In addition to this there are two small outliers, one in the neighbourhood of Great Livermere to the north of Bury St. Edmunds, and the other near Diss, in Norfolk. The primrose occurs round the margins of these areas, and, as is well known, hybridises freely with the Oxlip. There seems little reason to doubt that the restricted and peculiarly outlined habitat of the Oxlip in England is due to the fact that it is being gradually ousted by the more successful Primrose.

On the Continent the Oxlip appears to have as extensive a range as both Primrose and Cowslip (*P. officinalis* L.), being found all over Western and Central Europe, from Holland and France to S. Russia and from S. Sweden and Denmark to the Northern Alps.

Although the Primrose and Oxlip appear to be mutually exclusive in England, the Cowslip, on the other hand, grows freely throughout the Oxlip country, but hybrids between the two species are very uncommon. A few records of the cross *elatior* × *officinalis* aregiven by Pax[2] and are sometimes known as *P. media;* and Christy[3] mentions the finding of three probable Cowslip × Oxlip hybrids during the last eighteen years. The rarity of this cross is due partly no doubt to the common difference in habitat of the two species—the Oxlip living in the woods in England, and the Cowslip as a rule in meadows, but more probably to the difference in their times of flowering, the Oxlip usually being in full flower and getting over when the Cowslip is coming into blossom. On the Continent both species are often found freely intermixed[1] and this is also the case in the woods of the outlying district near Great Livermere, where the plant which forms the subject of this note was found.

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[1] Miller Christy. P. elatior in Britain, Journ. Linn. Soc. XXXIII., p. 172, with map.
Bailey. Journ. Bot., XLI., p. 145.

[2] Pax & Knuth. Pflanzenreich; Primulaceæ, pp. 60, 61.

[3] Miller Christy. l.c., pp. 197, 198.

This small outlier to the north of Bury contains at least two localities where Oxlips may be found. In one,—an overgrown swamp at the edge of a lake,—there are only Oxlips, and in the other,—a neighbouring wood on a gentle slope,—Primroses occupy the higher southern end, and also grow on the outskirts; whilst the northern lower portion is filled with Oxlips and Cowslips and numerous Primrose × Oxlip hybrids. It was in this wood that a single old plant of the Oxlip × Cowslip hybrid was found by the side of a broad path, and it was strikingly different from the Oxlips growing round it. The hybrid was discovered on the 26th of April, 1906, and had about half the flowers in the umbel expanded, whilst the Oxlips in the same locality were fully open. In its somewhat later flowering period the hybrid appears to be intermediate between the two parents. The leaves are firm and stiff on long petioles and are somewhat stiffly curved, which causes the lamina to lie either on the surface of the ground, or parallel to the surface (Pl. V., Fig. 1.) This character reminds one of the habit of the Cowslip,[2] as does also the obovate-oblong lamina, which is narrower than that of the Oxlip and longer than that of the Cowslip (Pl. V., Figs. 2 and 3); the serration of the margin is also intermediate in character between Oxlip and Cowslip. The upper surface of the lamina shews a velvety pile of short hairs like the Cowslip, but the hairs are longer than in that species, and, with regard to the under surface, it more nearly approaches the Oxlip.

The inflorescence characters are of considerable interest. In the Cowslip the scape bearing the umbel is stout, rather fleshy, and easily flexible (of white-buff colour), and covered with a short velvety pubescence (Pl. V., Fig. 3). In the Oxlip the scape is rather thin and wiry, stiff and erect, pale-green in colour, and covered with a tomentum of rather woolly hairs (Fig. 2). The hybrid shews the characteristic Oxlip scape, with a velvety tomentum and green colour (Fig. 1). The flowers of the umbel are pendulous, after the

[1] Kerner. Oester. Bot. Zeitsch. XV., p. 80.

[2] In the Oxlip the leaves tend to be erect.

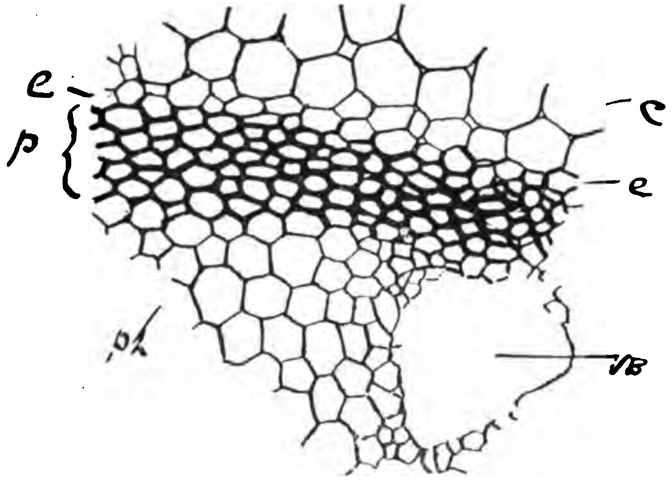
manner of the two parents, and are thus in striking contrast to the usual arrangement of the flowers in the Cowslip × Primrose hybrid. The calyx is about 16 mm. in length, slightly inflated, with the teeth about 7 mm. in length, triangular to oblong, acute to acuminate (Fig. 6). The teeth and sharp ribs are pale-green, like those of the Oxlip (Fig. 5), but the membranous portions of the calyx between the keeled mid-ribs are not so sharply differentiated as in this species. In the Cowslip (Fig. 7), the inflated calyx is uniformly coloured of a whitish pale yellow-green hue, varying in length from 9—15 mm., with teeth 4—5 mm., triangular, ovate, acute. In the Oxlip the calyx is from 10—13 mm. long, with teeth about 6 mm., narrowly triangular, acute to acuminate.

The corolla of the hybrid is a clear deep yellow, rather paler than the Cowslip, with a deep orange, 5-rayed ring at the throat like that of the Oxlip, with the limb saucer to cup-shaped as in the Oxlip. The lobes are obovate, subrotund, emarginate, being shorter and more rounded than those of the Oxlip. The scent of the hybrid approximates closely to the peculiar peach-like odour characteristic of the Oxlip.

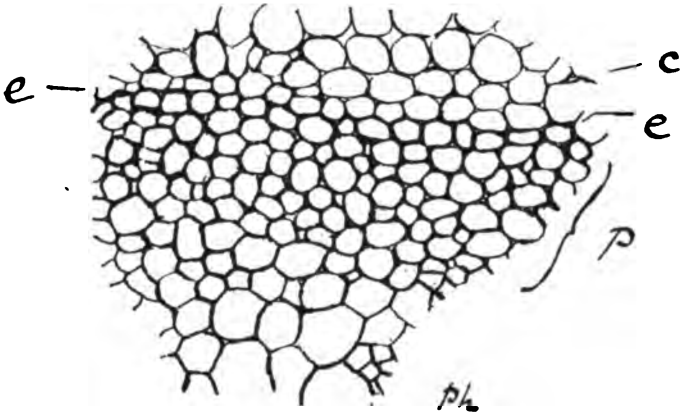
The Cowslip × Primrose hybrid or false Oxlip is of interest in comparison with our hybrid Cowslip × Oxlip. The leaves shew the surface-wrinkling characteristic of the Primrose with the velvety tomentum of the Cowslip (Fig. 4). The flower-scape is stout and Cowslip-like, but with a more dense tomentum (Figs. 4 and 8), and the umbel is composed of more or less erect flowers, shewing the Primrose "eye," and, like that of the Oxlip × Primrose, has a somewhat untidy scattered appearance, lacking the graceful drooping character of either the Cowslip or the true Oxlip.

An examination of the flower-scapes of the Oxlip, the Cowslip, and of the various Oxlip hybrids by means of transverse sections has yielded results of some interest.

The flower stem or scape of the Oxlip is found to possess a narrow band of thick-walled sclerenchyma, which is pericyclic in origin and forms a layer of tissue about five cells in depth just within the endodermis (Text-fig. 5). In the Cowslip, however, where the stem is usually of a greater diameter than in the Oxlip, the thickened band of the pericycle is much broader, and is composed of larger cells with thinner walls, which are only slightly lignified (Text-fig. 6). The sclerenchymatous tissue in this species forms a band some seven cells in thickness, and the greater flexibility of the Cowslip stalk is no doubt due to the slight amount of lignification of the walls.



Text-fig. 5. Transverse section of the flower-scape of the Oxlip. *c*, cortex; *p*,, pericycle; *e*., endodermis; *ph*., pith; *vb*, position of vascular bundle.



Text-fig. 6. Transverse section of the flower-scape of the Cowslip. Lettering as above.

The two scapes can thus be very easily recognized in transverse section. With regard to the structure of the scape in the various hybrids, it is found that the Cowslip has handed on its characteristic scape-structures to its hybrid with the Primrose, perhaps owing to the fact that the Primrose is practically acaulescent. For a similar reason no doubt the internal structure of the scape of the hybrid Oxlip Primrose shews all the characteristics of the true Oxlip. But in the Cowslip × Oxlip hybrid, where both parents have scapose umbels it is of interest to notice that the Oxlip stem-structure is dominant over that of the Cowslip, for the narrow band of thick-walled sclerenchyma is as well developed as in the Oxlip itself (cf. Figs. 1-4).

It is, of course, impossible to say whether the hybrid just described is a first cross between an Oxlip and a Cowslip or not, though the evidence seems to be in favour of this view. Its characters are more or less intermediate between those of the two parents, though the influence of the Oxlip appears to to be somewhat the stronger. In general hairiness, shape, and markings of the flower, and scent, as well as in the internal structure of its flower-scape, the Oxlip characteristics are predominant, whilst in the shape, position, and appearance of the leaves, and in the orange colour of the flowers, the influence of the Cowslip is clearly seen.[1]

The hybrids between the three species of *Primula* in Britain are of such interest that it is to be hoped that they will soon be subjected to careful scientific experiment. There can be no doubt that inter-crossing experiments will yield results not only of considerable interest as to the various forms found in a wild state, but will also throw important light on questions of hybridisation in general.

EXPLANATION OF PLATE V. ILLUSTRATING MR. A. W. HILL'S PAPER ON THE NATURAL HYBRID BETWEEN THE COWSLIP AND OXLIP.

Fig. 1. The Cowslip x Oxlip hybrid, *P. officinalis* x *elatior*; shewing the Cowslip-like leaves and the flowers and flower-scape more like those of the Oxlip, cf Fig. 6. The corolla is orange, and the calyx shews Cowslip characters.

Fig. 2. An umbel and leaf of the true Oxlip, *P. elatior* L., cf. Fig. 5. The corolla is of a pale cream colour with an orange ring. The calyx is contracted at the throat.

Fig. 3. An umbel and leaf of the Cowslip, *P. officinalis*, L., cf. Fig. 7. The corolla is deep orange with characteristic markings and the loose calyx has short blunt teeth.

Fig. 4. An umbel and leaf of the hybrid Cowslip x Primrose, *P. officinalis* x *acaulis*, cf Fig. 8. Note the wrinkled leaf and hairy flower-scape. The corolla is yellow, with the five spots of the Cowslip shewing on the star-like eye of the Primrose. The calyx is inflated and hairy.

Figs. 5—8 for a comparison of the floral characteristics of these four plants.

Fig. 5. Flowers of the Oxlip.

Fig. 6. The Cowslip x Oxlip.

Fig. 7. The Cowslip.

Fig. 8. The Cowslip x Primrose.

The photographs were taken by Mr. Allard Foreman of the Botanic Garden, Cambridge.

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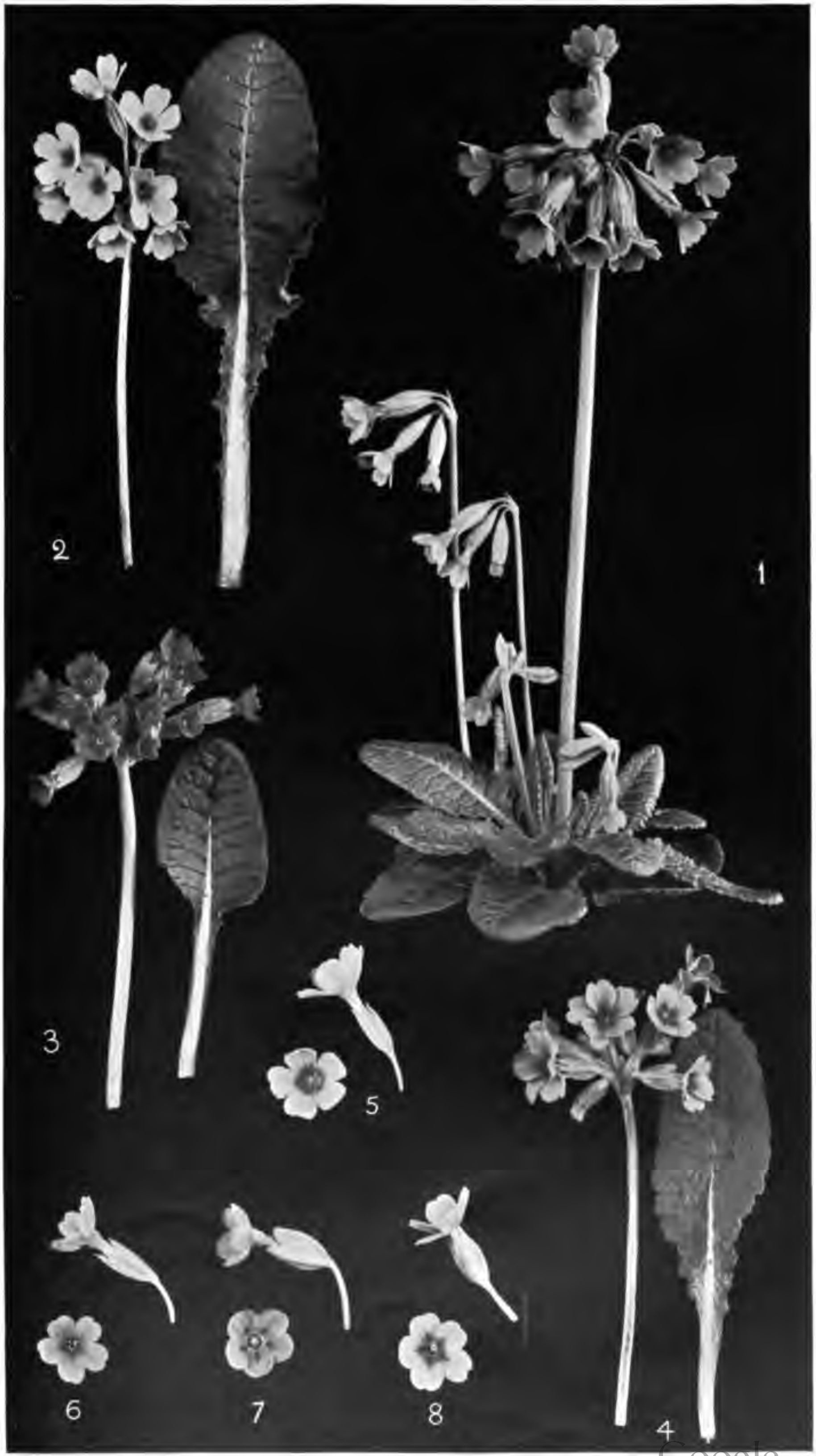
[1] Owing to the innumerable gradations between the Oxlip and the Primrose, which are found as natural hybrids, it is not possible at present to discuss the influence of each of the parents in the first cross.



A. W. HILL —— COWSLIP - OXLIP HYBRID.

OOGENESIS AND EMBRYOGENY IN *EPHEDRA DISTACHYA.*

BY
EMILY M. BERRIDGE, F.L.S. AND ELIZABETH SANDAY, B.Sc.

(Concluded from p. 134).

[Plates II. and III. accompanying this Paper were issued with the May Number.]

DEVELOPMENT OF JACKET CELLS AND ABNORMAL EMBRYOGENY.

IN a large number of ovules, however, this normal method of embryogeny appears to be superseded by another in which the jacket cells of the archegonium play a leading part. It may be well here to review the whole history of these cells from their first appearance simultaneously with the archegonium initials, since considerable attention has been devoted to them lately in work on other groups among the Gymnosperms.

The common origin of these cells and of the archegonium initials from a group of tubular alveoli in the apex of the embryo-sac has been mentioned before. At the time when the primary neck cells are being cut off from the initials, the tubular cells between the latter are undergoing a series of divisions and forming rows of jacket cells arranged in a regular manner. The likeness of these to the central cells, except in the matter of size, is apparent in Fig. 4. Such a similarity of origin and appearance in *Sequoia sempervirens*, has led Professor A. A. Lawson to the view that the jacket cells are sterile archegonium initials (9).

This tissue keeps pace with the growth of the central cell first by cell division, and later by individual growth of the cells. They soon become crowded with food material, and the nucleus divides into two by direct division long before this occurs in the central cells. Sometimes three nuclei are found in one cell, but the third is usually small or incompletely cut off. Strasburger, after describing this mode of direct division in the jacket cells of *Ephedra alte* briefly remarks that it is followed by division of the whole cell. This does not seem to be the case here, for the number of jacket cells does not increase to any extent after the appearance of this mode of division. The separation of the two nuclei is frequently incomplete, or one of them assumes a dumb-bell shape, which gives the impression that division is going on continuously.

The walls of these cells are very thin, but in deeply stained sections variations in their thickness are just perceptible along the cut edges. Also in surface view they show thin areas just like those figured in Miss Stopes, and Dr. Fujii's paper (3), while fine plasmic threads are constantly observed at points where the cytoplasm of the egg has separated from the wall. In the fully-grown, but unfertilized egg, colourless drops of a viscous appearance seem to be oozing through it into the archegonium; it is only after the time of fertilization that proteid vacuoles containing granules are seen to be passing through, and soon after the wall breaks up entirely in many places and allows the jacket nuclei to escape. Just at this time a curved row of pro-embryonal cells is found in the majority of ovules examined; these are similar to those developed from the daughter-nuclei of the oospore, that is, they possess large nuclei surrounded by radiating strands of cytoplasm and are bounded by delicate cell-walls, but they are situated in the middle and upper part of the egg-cell, and when first formed contain ill-defined masses of fusing nuclei, very different in appearance from the well-marked daughters of the fusion nucleus. Many circumstances seem to indicate that these pro-embryos arise from the escaped jacket nuclei and not from the fertilized egg nucleus. They are always found lying near empty jacket cells, and are always in contact on one side with the wall of the archegonium. One slide showed an archegonium containing two series of pro-embryos, one in the pointed base corresponding to that formed by what we have called the "normal" method of embryogeny, the other lying above it corresponding to the series just described (Fig. 16, cf. Fig. 14). The first or normal series of pro-embryos is evidently dwindling away, the second upper series is still in course of formation. At one point nuclei can be seen passing out of adjacent jacket cells to fill a gap in this series (Fig. 17), while at another the pro-embryo is simply an out-growth of one jacket cell lying in a row of others which are in a dying condition (Fig. 18).

The view that these pro-embryonal cells are formed by jacket cell nuclei, is supported by the fact that similar pro-embryos are frequently found within the jacket cells themselves, even when not adjacent to the archegonia. Such a pro-embryo is shown in Fig. 19, bounded on three sides by the disorganizing remains of an unfertilized archegonium and of the same and other jacket cells, and on the fourth by the vacuolate cells of the undifferentiated endosperm. Just prior to the formation of these pro-embryos, migration of nuclei is frequently found to occur in the jacket cell tissue; cases are shown in Fig. 20 where the wall between two neighbouring cells has clearly broken down, and the nucleus from one is passing through the gap and fusing with that of the other.

Mitotic division reappears at this stage among the jacket cell nuclei; it seems to result from the fusions of these nuclei, for in most cases, as in that represented in Fig. 21, a neighbouring cell could be found which is practically empty of contents, with the wall between them broken down. Also in this case forty-eight chromosomes could be counted, *i.e.*, twenty-four passing to each daughter-nucleus. This is the sporophyte number of chromosomes; in other instances too, the larger sporophytic number appears to be present. Early in the history of the ovule when the jacket cells are being formed, twelve is the number present, agreeing with that found in the reduction and following divisions of the pollen mother-cells. It could not be determined what part this spindle formation plays in the development of the uninucleate pro-embryonal cells, but probably the latter are formed from the daughter-nuclei.

Many of the jacket cells are at this time breaking up by a process of cleavage, their nuclei fragment, and cell walls grow in between the portions. A similar process is occurring in the archegonia, lines of cleavage appear in all directions in the cytoplasm, which becomes very dense. This condition only lasts a short time; as soon as the suspensors have developed, and embryos are beginning to be formed at their tips, all the food material from this region has been absorbed and the archegonia and surrounding cells appear quite empty.

A considerable number of these pro-embryonal cells break up in like manner eventually, particularly if they are some distance from the archegonia, and even of those close to and within the oospores, which put forth suspensors, comparatively few form embryos; the breaking up of the nucleus within some of them into a number of small nuclei again, as has occurred in Fig. 15D, is probably the commencement of disorganization.

Nevertheless, the power of these jacket cells to form pro-embryonal cells capable of giving rise to embryos cannot be doubted after an examination of these slides; thus we have here in the prothallium of a Gymnospermous plant a method of reproduction closely resembling that described by Messrs. Farmer and Moore and Miss Digby as occurring in certain so-called "apogamous" prothallia of ferns (10). In the case of *Ephedra*, however, the fusing jacket-cell nuclei may be sexual in nature; if so, a parallel can be drawn, perhaps, still more closely with those cases among the Uredineæ, where fertile cells have been shown by Christman and Mr. V. H. Blackman to fuse in pairs before giving rise to the æcidiospores (11). The fact that it is the pro-embryos in and adjacent to the archegonia which seem to have the best chance of forming embryos, raises the question whether the contents of the pollen-tube play any part in this method of embryogeny. The number of archegonia to which no pollen-tubes have found their way are comparatively few; in cases where tubes have undoubtedly entered, sometimes there is total failure to produce pro-embryos, usually owing to the disintegration of the egg-nucleus, and sometimes the "abnormal" series of pro-embryos is found. It seems quite possible that in these latter cases the contents of the tube may stimulate the jacket-cell nuclei to further development, or that some of the nuclei from it may fuse with them. In one instance this seems about to occur, a jacket cell nucleus being found in the act of breaking through into the egg-cell, close to one of a group of four pollen-tube nuclei lying in the apex of the archegonium; as yet no other jacket nucleus has escaped into the egg-cell. It is evident, however, from the number of pro-embryonal cells formed actually within the jacket cells that the direct stimulus of fusion with a pollen-tube nucleus is not essential to this development of pro-embryos.

Although this mode of embryogeny has been called abnormal, and regarded as possibly the result of adverse conditions, yet it seems not improbable, as far as can be gathered from M. Jaccard's account of embryo-formation in *E. helvetica* (2), which is not at all clear on many points, that the same kind of apogamy occurs in that species also. He speaks of the renewed activity of the jacket cells after the time of fertilization, and of the occurrence of mitotic division and considerable growth at that period, and remarks on the great likeness to small archegonia which they present. He aments the impossibility of distinguishing between certain "condensations protoplasmiques globuleuses" and the true daughter-nuclei of the fertilized egg-nucleus, and mentions in passing that these condensations are surrounded by definite zones of cytoplasm. These are probably the young pro-embryonal cells formed by the escaped jacket-nuclei. The young embryos which are described as arising directly from the pro-embryonal cells without any formation of tubular suspensors are spoken of as occurring amidst a tissue of cells at a very early stage; and the functional embryo is described and figured as lying at the base of a columella formed from the cells of the central region of the embryo-sac. A simple explanation of this situation of the embryos, which are said to arise directly from the pro-embryos, outside the archegonium is, that they have themselves been developed from jacket cells constituting part of the central column of tissue around which the archegonia are grouped, for it is just these cells which are often most active in forming abnormal pro-embryos in *E. distachya*.

If the jacket cells do assume the function of embryo-formation both in *Ephedra distachya* and *E. helvetica*, as appears to be the case, and this mode of embryogeny is not a mere occasional abnormality, we have within the limits of the genus an interesting transition series from a truly Gymnospermous organization of the ovule as described by Strasburger for *E. altissima* to a form which leads directly on to that of *Welwitschia*. A mere reduction in size of the egg-cells, and a failure of the primary neck-cells to divide more than once or twice, both of which conditions are occasionally found in *Ephedra distachya*, would result in the presence of a mass of tissue in the apex of the prothallium, nearly all the cells of which would be capable of fertilization by the pollen-tube. Such a condition is present in *Welwitschia*, for Professor H. H. W. Pearson in his recent paper regards all the cells of the fertile apical region as "potentially equal, though some do not produce prothallial tubes." These fertile cells in *Welwitschia* also show a marked resemblance to the jacket cells of *Ephedra*, in their multi-nucleate condition, which is believed to arise by the amitotic division of the original single nucleus. Should Professor Pearson's further investigations prove that a pro-embryonal cell is formed within the tubular cells after fertilization there will be little doubt that such cases as this among the species of *Ephedra* are real links between the typical Gymnosperms and this genus.

Also, though this much specialized, isolated group of plants is not, in all probability, in the direct line of descent of angiospermous plants, yet the embryogeny of this species of *Ephedra* does suggest a process of evolution by which the archegoniatæ may have given rise to forms in which the archegonium, as such, does not appear.

SUMMARY.

In *Ephedra distachya* the megaspores appear to be arranged in a tetrahedral, and not in a linear manner as in *E. trifurca*.

The integument arises first on the posterior side of the ovule, and only later anteriorly.

"Alveoli" are formed after a very large number of nuclear divisions, and the archegonial region already begins to be differentiated.

Cell-division occurs much more freely in the lower than in the upper part of the embryo-sac. The archegonial region becomes a mass of archegonium initials and jacket cells, distinguishable from the surrounding cells by their large nuclei and richness of cell-contents.

The pollen-chamber is formed by the breaking down, first of hypodermal, and then of epidermal cells at the apex of the prothallium. At its base the apical cells of the prothallium are exposed.

The species appears to be anemophilous though insects may occasionally pollinate the ovules. The grains are probably drawn down the micropyle into the pollen-chamber by the gradual drying up of the liquid secreted at this time.

The archegonia number from five to eight; until the central cell is full-grown the nucleus remains at the apex. The ventral canal nucleus appears to separate from the egg-nucleus by a process of direct division shortly before fertilization; no wall is formed between them.

The pollen-tube discharges the two male gametes enclosed in a common cytoplasmic sheath into the egg. The functional gamete slips from the sheath and passes to the egg-nucleus, but in most cases fusion does not appear to have occurred, and no case of the entry of the sperm into the egg-nucleus was found.

Fertilization, however, probably occurs occasionally, for archegonia are found containing nuclei which can only arise from the egg; some of these pass to the base of the archegonium and there form pro-embryonal cells. These form long suspensors, bearing embryos at their tips. Most of the pro-embryos, however, are formed by abnormal development from the jacket-cell nuclei.

The jacket cells arise at the same time as the central cells; at first they increase in number by indirect division. Later the nucleus divides by direct division and the bi-nucleate cell grows considerably larger and becomes full of food material. The wall of the egg-cell gradually becomes more and more permeable to food material, and finally breaks down, allowing the jacket nuclei to escape.

These nuclei fuse together within the egg-cell and give rise to pro-embryos.

In some cases the pro-embryos are merely enlarged jacket-cells which project into the archegonium.

In one archegonium both normal and abnormal pro-embryonal cells were found to be present. Pro-embryonal cells also occur within jacket cells which are not adjacent to the archegonia. Migration and fusion of the nuclei of neighbouring jacket cells precedes their formation. On dividing, these fusion nuclei show the sporophytic number of chromosomes.

It seems possible from Jaccard's account of *Ephedra helvetica*, that a similar development of the jacket cells occurs in that species also. Such development, if at all general in the genus, seems to indicate that, as in *Welwitschia*, a large proportion of the cells in the apical part of the prothallium are capable of fertilization and embryo-formation.

In conclusion we wish to thank Miss Benson for much kind help during the course of the work. Figures 3, 5 and 6 (Plate II.) are taken from drawings made by her during Miss Sanday's absence in South Africa.

University College,
London, 1907.

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EXPLANATION OF PLATES II. AND III. ILLUSTRATING THE PAPER BY MISS BERRIDGE AND MISS SANDAY ON "OOGENESIS AND EMBRYOGENY IN *EPHEDRA DISTACHYA*."

a.r , central cell of archegonium ; *j.c.* jacket-cell ; *p.t.*, pollen-tube ; *p.e.*, pro-embryo ; *e n.*, egg-nucleus ; *m.n.*, male nucleus ; *v.c.*, ventral canal nucleus.

Fig. 1. Tetrad of megaspores ; *m.*, functional megaspore. ×360.

Fig. 2. Longitudinal section of young ovulate strobilus. *n*, nucellus ; *i.*, integument ; *o.c.*, outer envelope ; *b*, *bract.*

Fig. 3. Longitudinal section of female "flower." *e.s.*, embryo-sac ; *a.*, archegonial region ; *n.*, nucellus ; *i.*, integument ; *o.e.*, outer envelope.

Fig. 4A. Young archegonium with primary neck-cell (*n*).

Fig. 4B. Tubular cell dividing into a series of jacket-cells.

Fig. 5. Sister archegonia probably derived from a single archegonium initial. ×98.

Fig. 6 Fully developed necks of two unfertilized archegonium. *d.*, products of degeneration of neck cells. *p.ch.*, pollen-chamber. ×174.

Fig. 7. Apex of archegonium with egg and ventral canal nuclei separating amitotically.

Fig. 8. (*a*) Small archegonium, (*b*) jacket cell, showing the resemblance of the egg and ventral canal nucleus in (*a*) to the pair of nuclei in (*b*).

Archegonium (*a*) is one of a pair of sister archegonia similar to those shown in Fig. 5.

Fig. 9. *Ephedra fragilis.* Ventral canal cell cut off from the apex of an archegonium. ×300.

Fig. 10. An archegonium, the apex of which has grown upward to meet the pollen-tube. *a.*, original position of the apex. ×120.

Fig. 11. A pollen-tube within the apex of an archegonium. *p.n.*, five small nuclei discharged from the pollen-tube. ×300.

Fig. 12 Male nucleus approaching the egg nucleus. ×300.

Fig. 13. A pair of male gametes; the functional gamete (*f.g.*) leaving the cytoplasmic sheath. ×600.

Fig. 14. A fertilized archegonium with normal pro-embryonal cells in its pointed base. ×125.

Fig. 15. Pro-embryos. *a* and *b* show the first division of the nucleus; *c.* shows a two-celled embryo, and appears to have arisen from a jacket cell ; *d.* is multi-nucleate, and also arises from a jacket cell. ×300.

Fig. 16. An archegonium containing both normal and abnormal series of pro-embryonal cells. ×130.

Fig. 17. Jacket-cell nuclei escaping into the archegonium of Fig. 17 and fusing to form a pro embryonal cell. ×236.

Fig. 18. Pro-embryonal cell formed by the outgrowth of a jacket cell belonging to the wall of the archegonium. ×360.

Fig. 19. Pro-embryonal cell formed within a jacket cell. *e.*, endosperm cells ; *a.*, degenerating archegonium. ×300.

Fig. 20. Migration of jacket nuclei. ×300.

Fig. 21. Nuclear spindle within a jacket cell. *n.*, remains of second nucleus of the jacket cell; *c.*, neighbouring cell from which the nucleus has migrated.

NOTES ON THE SPORE-BEARING ORGAN *CODONOTHECA* AND ITS RELATIONSHIP WITH THE CYCADOFILICES.

By E. H. Sellards.

[Text Fig. 7.]

THE spore-bearing organ, *Codonotheca*, was described in detail by the writer in 1903 from impressions in iron-clay concretions from Mason Creek, Illinois.[1] A few additional specimens contained in the museum of the University of Florida direct attention anew to this organ, and invite renewed comparison between this and other known spore-bearing organs. The following description is abstracted from the detailed account in the paper to which reference has been made.

The organ is a symmetrical cup- or bell-shaped body, made up of a circle of six equidistant, lamina-like, spore-bearing divisions. These, arising at a common level, unite laterally at the base, are free at the tips, and thus surround a central cavity. Each division is traversed on the inner or spore-bearing side by two strong vascular bundles, supplied by the dichotomy of six main strands. The union of the parts below forms a cylindrical base, while the whole organ is borne on a slender petiole. The base which seems to have consisted for the most part of an external envelope of non-resistant fleshy tissue, is usually more or less completely flattened in the fossil condition. It is traversed by lines often irregular and wavy, lying near the surface and extending along the dorsal side of the spore-bearing divisions, probably representing sub-epidermal strands of strengthening tissue. The fusion of the six main vascular strands forms a cone-shaped body pointed below, and large at the top where it breaks into bundles. This area occasionally retains its cylindrical shape (Text-fig. 7. 1). The six strands originating at a common level diverge and dichotomize also at approximately the same level. The twelve bundles thus formed pass into the six spore-bearing divisions or segments, each segment receiving one bundle from each of the two adjacent main strands (5). This arrangement of bundles is verified from numerous specimens and is significant as probably indicating that the six segments arose

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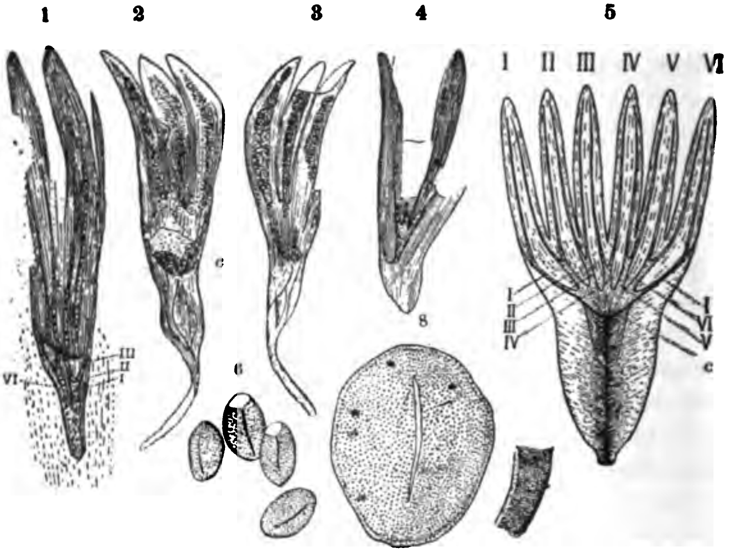
[1] *Codonotheca*, a New Type of Spore-Bearing organ from the Coal Measures. Amer. Journ. Sci., Vol. XVI, pp. 87-95, pl. VIII.

from the dividing up of an original disk. The free tips of the segments occasionally stand open, thus retaining in part their original shape, owing probably to their having been quickly buried in sediment. The average specimens of *Codonotheca caduca* measure 3 to 5 centimeters from base to tip. The width of the top is about 1⅓ centimeters. The segments above the point where they become

Codonotheca caduca, SELLARDS.



TEXT-FIG. 7.

1. The fleshy covering has disappeared by maceration from the base of this specimen, allowing the resistant area at the centre, which still retains its shape, to stand out prominently. Strands I., II., III. and VI., are visible, IV. and V. being hidden on the opposite side. Twice natural size.

2 and 3. Figures two and three illustrate the two sides of a single specimen. The very numerous large spores lie in a depressed channel along the inner side of the segments from the tip to the base. The cavity formed by the united bases of the segments ends at C. Natural size.

4. Specimen showing the fleshy base flattened and with the vascular cone at the centre. Natural size.

5. Plan of structure of the spore-bearing organ. The organ is represented as cut down the middle and laid open, the cut passing between the segments, hence in the basal part through one of the main strands. The end of the cavity is marked at C. Natural size.

6. Group of spores imbedded in a deposit of sphalerite, and with the surface ornamentation consequently well preserved. Enlarged 28 times linear.

7. Section through the spore wall, showing the thick outer, and a thin compact inner layer. Enlarged 200 times linear.

8. A single spore showing the slit as commonly observed. Enlarged 84 times linear. Author's illustrations.

free are 1½ to 2 centimeters long, and 2½ to 3 millimeters wide. The petiole is slender and long. Regarding the manner in which the organ was borne it was only possible at the time of writing the original description to state that "Two of the fossils lie side by side on one of the nodules in such a way as to indicate that both were probably attached by long petioles to a common stem. At one side, and at a slightly lower level, is seen a slender striated stem, but the actual connection is not observed." One of the new specimens now at hand shows several of the spore-bearing organs lying on either side of a central stem, those toward the top being reduced in size. Although the preservation is not perfect, still the relation of the several organs to each other and to the central stem is such as to leave scarcely a doubt but that they are borne by terminal divisions, and are attached by slender petioles to the central stem.

The spores lie, as seen in impressions of well preserved mature specimens, over the inner surface of the segments from base to tip, and are confined to a more or less well-marked depression occupying from one-half to two-thirds of the width of the segments. The spores are large, elongate eliptical, 0·29 to 0·31 millimeters long, 0·18 to 0·20 millimeters wide, and of a brownish colour. There is no grouping of the spores or other indications of the location of sporangia, which were doubtless more or less completely immersed in the tissue, the dividing walls probably disappearing at maturity.

In connection with the original description *Codonotheca* was compared with all types of spore-bearing organ known at that time with which it could apparently have any possible relations. The type was regarded as not probably referable to any one of the better known classes of plants, but possible to the class of Cycadofilices, the fructification of which was but imperfectly known. The *Calymmatotheca Schimperi* of Stur, and *Aphlebiocarpus* Stur were mentioned as forms possibly related. Kidston's specimens of *Neuropteris heterophylla* were also mentioned as evidence of the dimorphic character of the Neuropterid group. The resemblance of the spores of *Codonotheca* in size and shape to the spores (pollen-grains) of *Dolerophyllum* was noted. The intimate association of *Codonotheca* at the Mason Creek locality with the large pinnuled Neuropteris, *N. decipiens*, led to the suggestion that *Codonotheca* may be the spore-bearing organ of this particular genus and species of Cycadofilices.

The conclusions thus very tentatively stated in 1903 were later more definitely formulated. In a letter to Professor F. W. Oliver, under date of January 27th, 1905, the writer expressed the belief that *Codonotheca* is the "male spore-bearing organ of the Neuropteris type" of Cycadofilices. In a letter to Mr. David White, dated March 20th, 1905, the writer expressed the belief that some one of the seeds at Mason Creek and *Codonotheca* would ultimately be found to represent respectively female and male fruits of the Cycadofilicinean genus and species *Neuropteris decipiens.* Similar views were expressed to other palæontologists. The several important new types of fructifications since described by various writers from the early deposits appear to the writer to lend support rather than discouragement to the hypothesis of the Cycadofilicinean relations of *Codonotheca.*

ON THE ASSIMILATORY TISSUE OF MANGROVE SEEDLINGS.

BY MADELINE CARSON, B.SC.

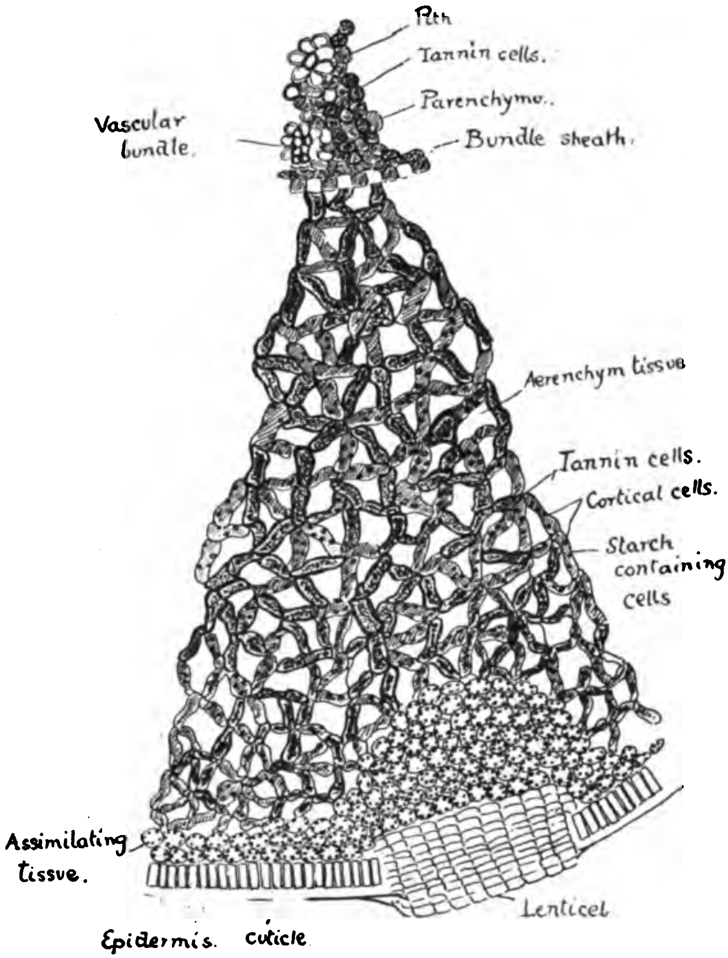
[TEXT-FIGS. 8—10.]

IN making a study of some seedlings of *Rhizophora* and *Bruguiera* my attention was drawn to their mode of nutrition. As is well known, the seedlings of these and other mangrove plants remain attached to the fruits for a considerable time, during which they obtain their food from the parent plant. In *Bruguiera,* according to the researches of Haberlandt[1], the endosperm consists of the cells, some of which form a connection with the cotyledons and with the ovular integument by haustorial processes.

But, as this method seemed to me not sufficient to provide all the food material necessary for so large a seedling, often attaining a length of a foot or more, I concluded that the seedling itself might undertake some carbon assimilation particularly as Professor Weiss, who gathered the seedlings at Mombasa, informed me that when fresh they had distinctly green colour beneath the yellowish epidermis.

[1] Haberlandt G. Die Ernährung der Keimlinge und die Bedeutung des Endosperms bei viviparen Mangrove-pflanzen. Annales du Jardin de Buitenzorg, Vol. XII., 1895.

Schimper[1] on the contrary, throws doubt on the assimilatory function of the stem of the embryo, since it is covered with a very thick cuticle, and since assimilatory tissue if present is very small in amount. The former assumption does not seem convincing since we know there are many leaves provided with thick cuticles which do assimilate. Goebel in his Pflanzenbiologische Schilderungenp acknowledges the assimilatory function of these stems, as does also Haberlandt (loc. cit.), but neither of these observers gives a detailed description of the assimilating tissue. It seemed to me therefore of some interest to examine the structure



Text-fig. 8. *Bruguiera* sp. Part of transverse section of stem.

---

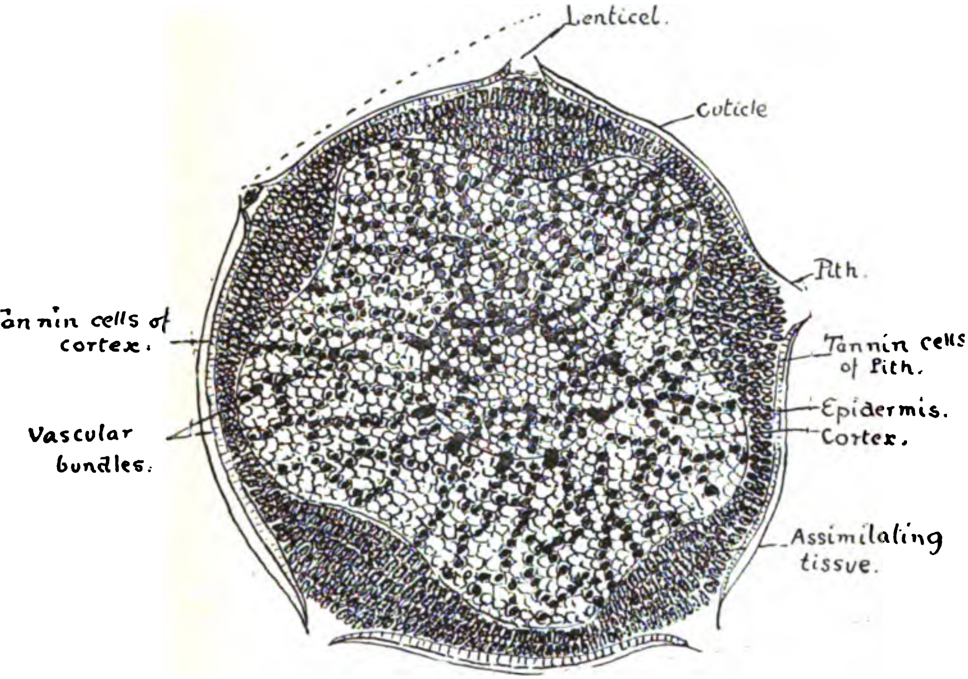
[1] Schimper A. F. W. Die Indomalayische Strandflora, 1891.

of the seedling, particularly of the hypocotyledonary stem, with the view of ascertaining whether any portion of its tissues was particularly modified to fulfil the function of carbon assimilation.

I first selected *Bruguiera* for examination. A transverse section about the middle of the hypocotyl revealed the following structures (Text-fig. 8). In the centre the pith was well developed and consisted of ordinary soft parenchymatous cells. Among these were scattered numerous cells with brownish contents. On the addition of iron salts these cells became dark green to black in colour and evidently contained tannin. At the edge of the pith were numerous small vascular bundles, containing only three or four xylem elements, and outside these a few phloem elements. The vascular bundles were separated from the cortex by a definite row of cells which might be regarded as a bundle sheath. The cortex contained an anastomosing network of tannin cells, and among these were seen many cells which did not stain for tannin, but contained abundance of starch grains. There were very numerous intercellular spaces, that is the cortex was lacunar, resembling in general character the aerenchyme tissue in the older breathing roots, although the aerenchyme tissue was not developed to such a marked degree. In sections stained with methylene blue the tannin containing cells made a conspicuous network. Other sections were stained with methylene blue and safranin. In these sections it was found that the tannin cells still took the methylene blue stain and made a ramifying network, while the protoplasmic contents of the other cells stained red.

Boiling unstained sections in water in order to dissolve out the tannin, very curiously turned the cells pink, so that even in an uncoloured section the course of the tannin containing cells and starch containing cells could be traced. The hypodermal cells were small, while the epidermal cells were large, elongated and contained tannin. In longitudinal section these tannin cells could be seen in definite strands which branched and anastamosed throughout the length of the stem. As one would naturally expect to find in a xerophytic plant the cuticle was very thick.

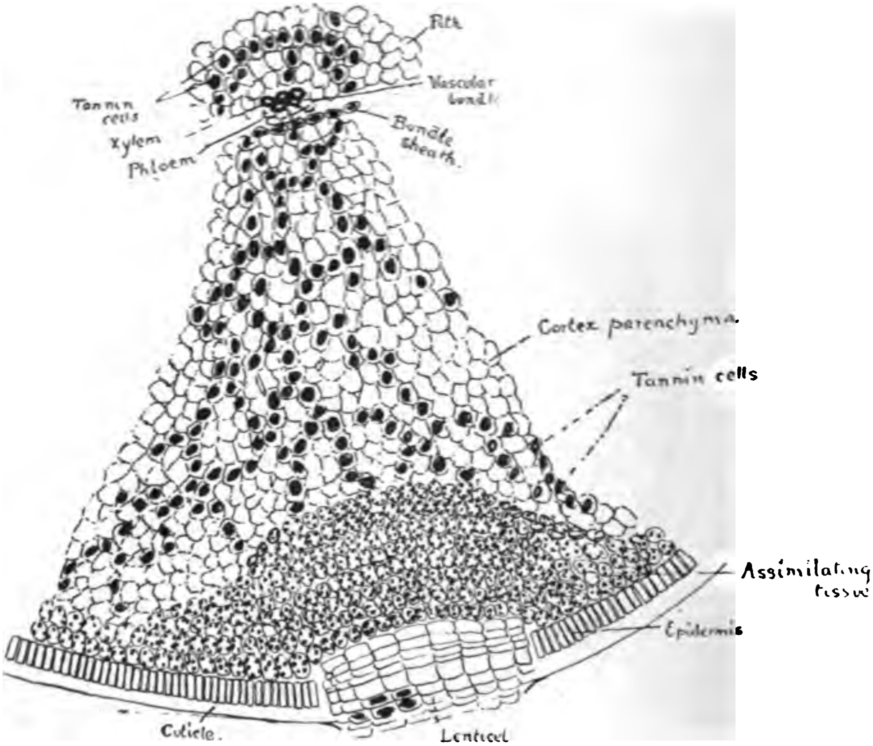
For a long time I was unsuccessful in finding either stomates or lenticels, or any place where air could enter the tissues. Removal of a complete plant from alcohol to water and examination under a strong lens, showed that drops of liquid exuded from the plant, in certain definite lines along its whole length, to within half an inch from the tip of the stem. It was found that the surface was not completely smooth, but was slightly ridged. It was on these ridges that the openings were found. Small strips of epidermis were removed from these ridges and examined under the microscope. It was found that the openings were on small tubercles. Some of these openings were connected with lenticels, but others were not. After cutting many transverse sections one or two containing stomata were found. On double staining with safranin and methylene blue, the guard cells stained red, while the rest of the epidermal cells were blue.



Text-fig. 9. *Rhizophora*, sp. Semi-diagrammatic sketch of a transverse section of the hypocotyl.

In addition to the above mentioned structures it was found that ordinary chlorophyll containing tissue was developed. This was not distributed in a regular layer round the stem under the epidermis, but varied in thickness in different parts. Near the stomates or lenticels there were usually from six to eight rows of assimilating cells chlorenchyma, but in other parts there were generally only two rows. As in a complete transverse section there were usually four or five lenticels, it follows that the total amount of assimilating tissue in the whole stem was not inconsiderable.

The next specimen examined was *Rhizophora* (Text-figs. 9 and 10). In general structure it resembled *Bruguiera* and gave the same results on staining. There were certain minor differences in the structure of the cortex. Here the cells were not so elongated in the radial direction as in *Bruguiera*, and the cortical air spaces were not so well marked. Otherwise the arrangement of tannin containing and tannin free-cells in the cortex was similar, as also was the distribution of assimilating tissue. These species had also a well developed cuticle.



Text fig. 10. *Rhizophora*. Part of transverse section of the hypocotyl.

In the specimen examined, only one section containing a stomate was obtained. It was not in an elevated position but was slightly sunk. Lenticels which were very numerous were always found on small tubercles. The stomate opened into a distinct chamber surrounded by assimilating tissue.

Two other species of *Rhizophora* were examined and similar results were obtained. The structure was similar to that of the *Rhizophora* obtained from Mombasa.

Although perhaps this study was not a very exhaustive one, it is probably safe to assume that in the Rhizophoraceae generally the hypocotyl is an assimilatory organ, and is definitely modified for assimilatory purposes, and this is certainly true for the species investigated.

In conclusion I wish to say that my thanks are due to Professor Weiss, who supplied me with material, and from time to time kindly gave suggestions as to the method of doing this work.

XEROPHILY AND THE DECIDUOUS HABIT.

THE communication of Miss Stopes[1] on the Xerophily of the Coniferales, raises several interesting matters. With her general contention, that the xerophily of the Coniferales is inherited and not acquired, I do not propose to deal, as Miss Stopes amply proves her case. There is, however, an important modification of this argument to be made before it can be regarded as applicable to the whole family; and there is, running through the whole of Miss Stopes's article, an assumption with which I do not agree.

This assumption is that the xerophily of the Coniferales is more pronounced than the xerophily of deciduous dicotyledonous trees, that the xerophily of the Coniferales is out of place at the present time in a mixed, deciduous forest. For my part, I regard the Coniferales as possessing one particular kind of xerophily, and the deciduous, dicotyledonous trees as possessing another; and the xerophily of the latter species appears to me to be quite as effective as, if not, in fact, more effective than the xerophily of the former species. The xerophily of the Coniferales, is seen, as Miss Stopes points out, in the "xerophytic leaf," and in the whole structure of the wood, especially in the small diameter of the tracheides. The xerophily of the dicotyledons, I maintain, is seen in the deciduous habit, which, during the winter season, reduces transpiration to zero.

Taking the Scots pine (*Pinus silvestris*) and the birch (*Betula alba*) as well-known British examples of the conifers and the dicotyledons respectively, it is found that *Betula* ascends to higher altitudes and reaches higher latitudes than *Pinus*. As the two species often occur as associates in identical situations, this distribution[1] suggests that the xerophily of *Betula* is more effective than the xerophily of *Pinus*.

---

[1] Stopes, M. C. "The Xerophily of the Coniferales," NEW PHYTOLOGIST, February, 1907.

Rikli,[2] discussing the vegetation of Corsica, gives the conifer zone of that island as between 800 and 1,200 metres. In the lower part of this zone, *Pinus Pinaster* is dominant, *P. Laricio* in the upper. Above the conifer zone, however, Rikli records a beech zone. In the lower part of the beech zone *P. Laricio* is present; but the deciduous beech (*Fagus sylvatica*) reaches 1,400 metres, an altitude which is not attained by the evergreen pine (*P. Laricio*).

Again, among the conifers themselves, it is the deciduous species of *Larix* that reach the farthest north. Cajander[3] records species of *Larix* at 70° N. on the river Lena, and this latitude is not reached by any of the more numerous, evergreen conifers.

The same phenomenon is seen amongst the dicotyledons themselves. The distribution[1] of *Calluna*, with its markedly "xerophytic leaf," is less wide than that of *Vaccinium Myrtillus*, with its so-called "mesophytic leaf"; and, further the deciduous *Vaccinium* reaches a much higher altitude than the evergreen *Calluna*, although these plants frequently occur side by side.

Again, confining attention to a single dicotyledonous genus, each of the two deciduous members of the genus *Vaccinium* (*V. Myrtillus* and *V. uliginosum*) possesses a wider distribution[1] and ascends to a higher altitude than any evergreen member of the genus (e.g., *V. Vitis-Idæa*); and similarly the deciduous oaks (e.g., *Quercus Robur*) ascend to higher latitudes and altitudes than the evergreen oaks (e.g., *Q. Ilex* and *Q. Suber*).[4]

These examples are taken from species which are ecological and systematic allies respectively; and the facts appear to support my view that the deciduous habit is a more effective form of xerophily than the "xerophytic leaf" and "xerophytic wood" of the conifers. The facts also suggest that when xerophily is under consideration, the habit as well as the structure of plants must be taken into account.

---

[1] Smith, R. "Plant Associations of the Tay Basin"; I., *Proc. Perthshire Soc. of Nat. Sci.*, 1898; II., *Ibid.*, 1900.

[2] Rikli, M. "Botanische Reisestudien auf einer Frühlings fahrt durch Korsica." Zürich, 1903.

[3] Cajander, A. K. "Studien über die Vegetation des Urwaldes am Lena-Fluss." Helsingfors, 1904.

[4] Flahault, C. "Essai d'une Carte botanique et forestière de la France." *Ann. de Géogr.*, 1897.

Hence I do not regard the undoubted xerophily of the Coniferales as out of place at the present time, or out of touch with modern requirements. On the contrary, I regard the primitive and general xerophily of the Gymnosperms, transmitted to the modern conifers, as an important factor which enables the latter plants to hold their own in the deciduous forests of the north temperate zone, and as being necessary for the continuance of the conifers in a region, which, for more than half the year, is ecologically xerophytic.

With regard to Miss Stopes's general conclusion, that the xerophily of the Coniferales is phylogenetic and not adaptive, it appears to me that the acicular leaf of many northern species of conifers, and the deciduous habit of a few others, furnish important exceptions to the truth of the dictum. It is usually admitted that the broad-leaved conifers are more primitive than their needle-leaved relatives; and it will not be denied that the deciduous species of conifers are more recent than the evergreen members of that order. I see no difficulty in regarding both the acicular leaf and the deciduous habit of certain conifers as due to environmental factors. These two forms of xerophily, instead of being out of place at the present time, may be regarded as factors which account for the present wide and general distribution of northern conifers; and, instead of needing to be explained away, they are precisely the factors which furnish a partial, if not indeed an adequate and a sufficient explanation of the frequent dominance and successful competition of northern conifers among phylogenetically higher forms.

There is a further question into which I have not entered, namely, what is xerophily? It appears to me that no satisfactory answer to this question has yet been given by any botanist. It is not sufficient to quote figures relating to the amount of water lost during transpiration. At best, such figures are only comparative, and there is no accepted standard of comparison. Before a solution of this problem is found, a great deal of research is necessary, not only along conventional lines, but also by methods which, at present, are foreign to the laboratories of the schools.

Manchester, C. E. MOSS.
May 29th, 1907.

RECENT APPOINTMENTS.

Mr. V. H. Blackman, M.A., Lecturer in Botany at the Birkbeck College, has been appointed to the new Chair of Botany at the University of Leeds, and Mr. D. T. Gwynne-Vaughan, M.A., Lecturer in Botany at Queen Margaret College, Glasgow, will succeed Mr. Blackman at the Birkbeck College.

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VOL. VI., No. 8. OCTOBER 31ST, 1907.

THE NEW PHYTOLOGIST

A BRITISH BOTANICAL JOURNAL,

EDITED BY A. G. TANSLEY, M.A., F.L.S.

UNIVERSITY LECTURER IN BOTANY, CAMBRIDGE.

Contents:

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THE MEETING OF THE BRITISH ASSOCIATION AT LEICESTER.

BOTANICAL APPOINTMENTS.

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VOL. VI., No. 8. OCT. 31ST, 1907.

LECTURES ON THE EVOLUTION OF THE FILICINEAN VASCULAR SYSTEM.[1]

BY A. G. TANSLEY, M.A.

(University Lecturer in Botany, Cambridge).

LECTURE VI.

THE EVOLUTION OF DICTYOSTELY. POLYCYCLY.[2]

[FIGS. 51—64.]

IF we start from the condition of solenostely (Fig. 51) and consider the evolution of dictyostely (Fig. 52), we realise at once that as soon as two successive leaf-gaps overlap, either by crowding of the leaf-insertions, or by the prolongation forward of each leaf-gap till it passes the base of the next trace, the stele technically ceases to be a solenostele on Gwynne-Vaughan's definition (p. 152), and becomes a simple *dictyostele*,[3] defined as an amphiphloic cylinder in which at least some transverse sections show two or more leaf-gaps.

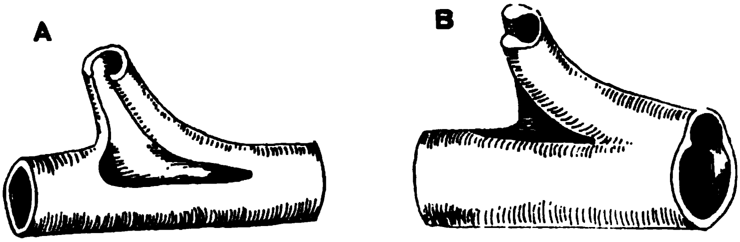

Fig. 51. Solenosteles, nodal portions, seen from dorsal side of rhizome, showing leaf-gaps and bases of leaf-traces. A. *Dennstædtia punctiloba.* B. *Microlepia speluncæ.* After Gwynne-Vaughan.

---

[1] A Course of Advanced Lectures in Botany given for the University of London at University College in the Lent Term, 1907.

[2] The present lecture is largely based on the work of Gwynne-Vaughan ('03).

[3] Brebner ('02).

Dorsiventral Types of Dictyostele.

Of course the simpler forms of dorsiventral dictyostele differ very slightly from a dorsiventral solenostele in which one leaf-gap nearly reaches to the insertion of the next trace (Fig. 52, A and B). When the gaps overlap for most of their length the dorsal internodal portion of the solenostele becomes reduced to a strip or strand (meristele) running obliquely across between two successive leaf insertions from one margin of the large ventral portion of the stele to the other (*d.m.*, Fig. 52, B). Such a structure is found in species of *Nothochlæna*, *Pellæa* and *Adiantum*. In *Cheilanthes lendigera* and *microphylla* a form even nearer the solenostele is found, for here, so far as the endodermis and pericycle are concerned, each leaf-gap in the stele is closed up before the next gap above is formed, but the gap in the xylem ring remains open till the next leaf-gap is reached, so that a small separate xylem strand is formed in the thickness of the stelar wall, crossing over between two successive nodes from one edge of the open xylem cylinder to the other.

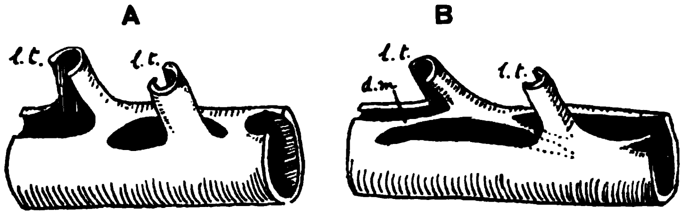

Fig. 52. Evolution of Dictyostely. *l.t.*, leaf-trace; *d.m.*, dorsal meristele. The mid-dorsal line runs between the two leaf-traces.

A. *Nothochlæna Marantæ.* Each leaf-gap just fails to overlap the next.

B. *Pellaea rotundifolia.* Each leaf-gap is prolonged forward so as to overlap the next. After Gwynne-Vaughan.

In the more completely dictyostelic Ferns the vascular structure becomes considerably more complicated, but in most cases the manner of its origin from the solenostelic condition is essentially similar to that already described, though the details may differ considerably. For instance in *Asplenium scandens* the internodes are long and the course of the dorsal meristele, as it runs across from one margin of the ventral meristele to the other, is very oblique. If the dorsal meristele were to pursue a straight longitudinal course, and instead of coming into bodily contact with the ventral meristele as in Fig. 52, B, it were to make connexion with the ventral meristele at the same points by means of short transverse commissures (*c*, Fig 53, A, B), a structure would result such as is actually found in very many dorsiventral Ferns. In most cases, however, the connexions with the simpler types are to some extent obscured by the fact that in place of a single leaf-trace two or more separate strands are given off to each leaf, and these usually run forward for a greater or less distance in the leaf-gap before turning out into the petiole (Fig. 53, 54, A). The dorsal and ventral cauline meristeles are generally clearly distinguishable from the leaf-traces by their greater breadth. Often, however (e.g., *Platycerium alcicorne*), the ventral meristele is broken up into an irregular meshwork of strands (Fig. 53, B), and these are very frequently no

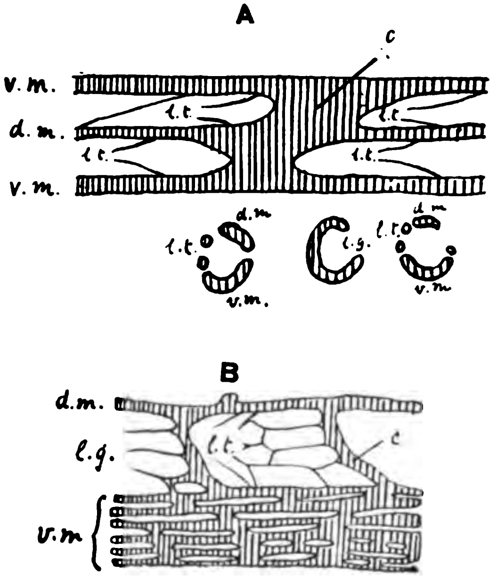

Fig. 53. Diagrams of relatively simple dorsiventral dictyosteles. *d.m.*, dorsal meristele; *v.m.*, ventral meristele; *c.*, commissure connecting the two; *l.t.*, leaf-trace; *l.g.*, leaf-gap. After Mettenius.

A. *Asplenium obtusifolium* The vascular system is supposed to be divided longitudinally along the mid-ventral line, and spread out so that the two halves of the ventral meristele appear at the top and bottom of the figure. Three diagrammatic transverse sections are placed opposite the points at which the sections are taken.

B. *Platycerium alcicorne.* One half of vascular system, seen from the side. The ventral meristele is seen to be perforated so as to form a meshwork.

thicker than the constituent strands of the leaf-trace (Fig. 54, A, B), so that the whole wall of the dictyostele is resolved into a number of branching and anastomosing strands, in which the distinctive parts of the original solenostele are lost and almost the only recognisable regions are the exits of the groups of leaf-traces. The dorsal meristele, however, usually retains its individuality, remaining stouter than the other vascular strands (Fig. 54, A, B). Sometimes it pursues a perfectly straight course, but often it bends from side to side in front of the successive leaf-gaps (Fig. 54, B) as in the more primitive forms.

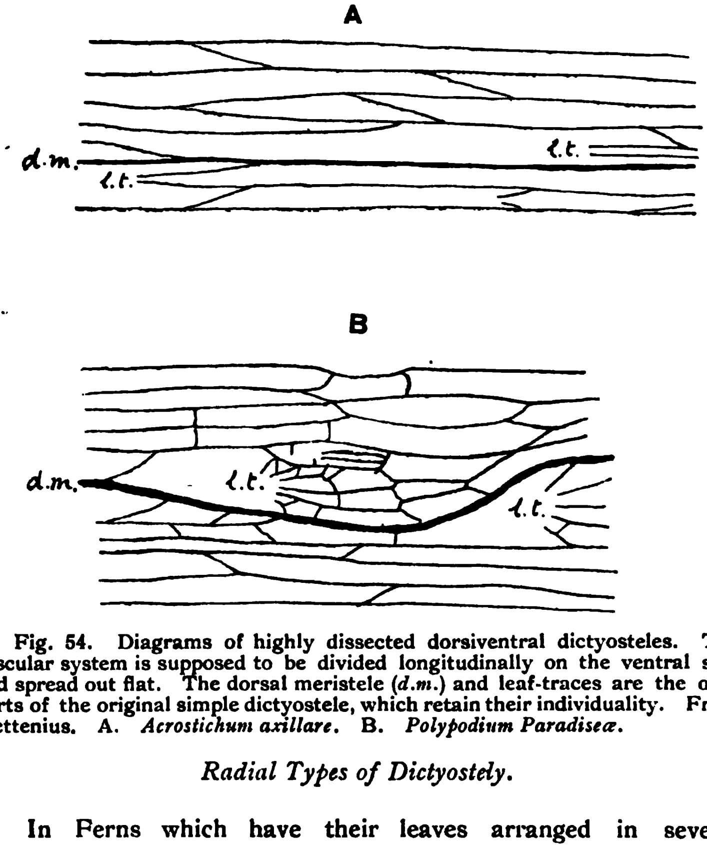

Fig. 54. Diagrams of highly dissected dorsiventral dictyosteles. The vascular system is supposed to be divided longitudinally on the ventral side and spread out flat. The dorsal meristele (*d.m.*) and leaf-traces are the only parts of the original simple dictyostele, which retain their individuality. From Mettenius. A. *Acrostichum axillare*. B. *Polypodium Paradiseæ*.

Radial Types of Dictyostely.

In Ferns which have their leaves arranged in several orthostichies round a prostrate or erect stem, three or more leaf-gaps usually overlap at a given level, and the solenostele is broken up into as many more or less equivalent meristeles arranged in a ring round the axis. If the structure is still but little removed from solenostely it may happen that two leaf-gaps only overlap at any one level, and then the vascular arrangement, seen in transverse section, generally consists of a large gutter-shaped meristele with another small one lying across its opening (Fig. 55, A). Although his structure is very similar in appearance to that presented by the simpler forms of the dorsiventral type, it must be remembered that in the radial type the relative position of the two meristeles changes as the phyllotactic spiral is passed through, whereas in the dorsiventral type it is constant. *Dicksonia Barometz* (Fig. 55, B) and various species of *Pteris* are examples of this form of stele.

As in the dorsiventral forms the leaf-trace generally consists, in the simpler types, of a single strand (though it often breaks up very soon into two – Fig. 55, A—or more petiolar strands), but sometimes it consists of two similar portions from the first (*Pteris tremula*, *Adiantum trapeziforme*). In the more advanced forms, *e.g.*, in the well-known case of *Aspidium Filix-mas* (Fig. 56), each leaf-trace consists of a number of similar strands arising from the cauline meristeles forming the sides of the leaf-gap.

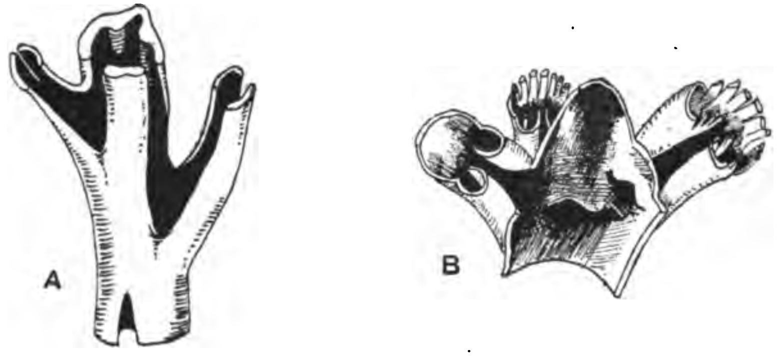

Fig. 55. A. *Gymnogramme calamelanos.* Radial stele showing two overlapping leaf-gaps.

B. *Dicksonia Barometz.* Part of stele cut longitudinally and seen from inside, showing three leaf-traces with very short leaf-gaps, through one of which the plane of section passes. After Gwynne-Vaughan.

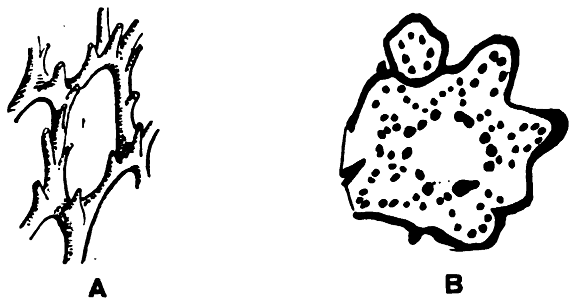

Fig. 56. *Aspidium Filix-mas.* A. Part of vascular system showing the overlapping of several leaf-gaps and the polydesmic leaf-trace.

B. Transverse section of stem showing the central ring of larger cauline strands and numerous leaf-traces in the cortex.

In a good many of the more advanced dictyosteles described, both of dorsiventral and radial type, and in some solenosteles also, there are of course gaps in the cylinder which are not leaf-gaps. To all such steles I should propose to apply the term *perforated*.[1] This perforation may perhaps be regarded in a general way as a reduction-phenomenon, the failure to develop vascular tissue where it is not wanted leading to the formation of a gap in the cylinder-wall, through which the ground-tissue of the pith is continuous with that of the cortex. But of the conditions of such gap-formation in any given case we know practically nothing. The splitting up of the original curved leaf-trace into two or more separate strands is also no doubt somewhat the same phenomenon. To this we shall have to return in a subsequent lecture.

REDUCED SOLENOSTELES AND DICTYOSTELES.

Some of the higher Ferns show aberrant types of solenostele and of simple dictyostele, which are regarded both by Jeffrey and Gwynne-Vaughan as reduced from the typical structures. *Antrophyum semicostatum* (and, according to Poirault, other species also) has a solenostele in which the phloem is present in a normal condition on the outer surface and passes round the edge of the leaf-gap, but quickly disappears on the internal surface of the vascular ring (Fig. 57, A). In *A. reticulatum*, also, the internal phloem is absent except on the margins of the leaf-gaps. Jeffrey

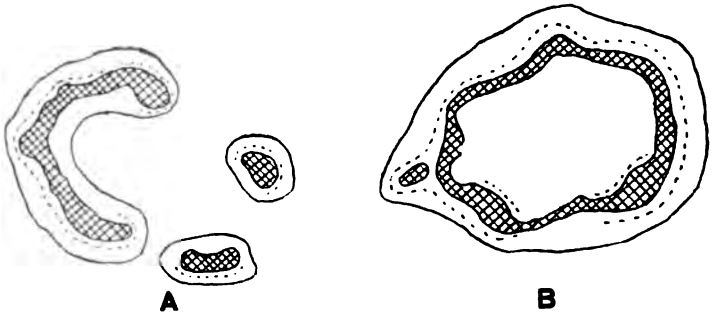

Fig. 57. A. *Antrophyum semicostatum*. Diagram of transverse section through leaf-gap. The stele and the two leaf-trace strands have no phloem on the inner side of the xylem.

B. *Antrophyum plantagineum*. Diagram of transverse section through internode. Internal phloem is absent except a little on the ventral side of the stele.

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[1] When the parts of the stele (meristeles) left between the perforations are reduced to thin strands (Fig. 54) the steles may be said to be "dissected."

states that there is no internal endodermis, but Gwynne-Vaughan finds that the plant is dictyostelic. In *A. plantagineum* both these authors agree that there is no internal endodermis, though the "pith" is histologically unlike the cortex. A little internal phloem is present on the ventral side of the stele (Fig. 57, B). In the genus *Vittaria* similar phenomena are met with. In *V. stipitata* the "decurrent ground-tissue" forming the pith decreases downwards through the internode, and in the specimens examined by Gwynne-Vaughan, is not continuous with that belonging to the node below. In this respect the plant resembles *Wibelia pinnata* (see p. 146), but there are facts which suggest reduction. Thus there are two strands of the leaf-trace, one departing from each side of the foliar gap. The stele is very small, the xylem-ring has a thickness of one or two tracheids only, and, unlike *Wibelia*, is equally narrow on all sides. Further, the pith is not surrounded by internal phloem, which is present in very small quantity, and is absent from the ventral side of the stele. The ground-tissue pith, as it dwindles, is replaced by tissue like that of the pericycle, suggesting a replacement of internal phloem in the course of phylogeny.

Facts of this kind naturally lead to the belief that the *Schizæa*-stele also has originated by reduction from solenostely (see p. 154), and this is certainly a possible view, though there is absolutely no evidence in *Schizæa* of internal phloem, and it is at least equally possible that here there has been a direct derivation from a solid protostelic form.

POLYCYCLY.

In a good many Ferns the vascular tissue is not confined to a single cylinder of haplostelic, solenostelic, or dictyostelic construction, but appears as two or more concentric cylinders or systems of strands. To all such structures the term *polycyclic* may be applied, as opposed to the much more frequent, and certainly primitive *monocyclic* condition.

The polycyclic condition is sometimes found as a special development in certain species of an otherwise monocyclic genus, while in other cases, notably in Matoniaceæ, Cyatheaceæ and Marattiaceæ, it is characteristic of a whole family or group. It is no doubt a response to a need for an increased vascular supply when for one reason or another this is not obtained by a mere increase in the diameter of the stele.

Solenostelic Types.

It is to Gwynne-Vaughan's beautiful researches on the solenostelic ferns[1] that we owe the discovery and elucidation of the first beginnings of the polycyclic condition in a series of species belonging to the genus *Dennstædtia*, a discovery which provides the morphological key to the great majority of cases of polycycly, whether occurring in solenostelic or in dictyostelic types.

The simplest case is found in *Dennstædtia apiifolia*. This fern possesses a typical solenostele, but with a very decided thickening of the xylem of the leaf-gap margin, which is often twice as thick as other parts of the xylem cylinder. In *D. adiantoides* (Fig. 58, A) the thickening of the xylem of the leaf-gap margin projects markedly towards the axis of the stem and further is not confined to the region of the leaf-gap, but is continued as a ridge along the internal surface of the vascular cylinder, throughout the whole length of the internode from one leaf-gap margin to the next. The additional xylem elements become separated as a distinct strand of xylem in the internode, and this is sometimes surrounded by a distinct phloem sheath of its own. The detachment reaches its maximum towards the upper end of the internode, while the additional xylem is most completely fused with that of the main vascular ring towards the upper end of the leaf-gap. In *Dipteris conjugata* there are rather similar thickenings of the leaf-gap margin, but these are practically separated from the tissue of the vascular cylinder by ground-tissue. In *Dennstædtia rubiginosa* (Fig. 58, B) there are

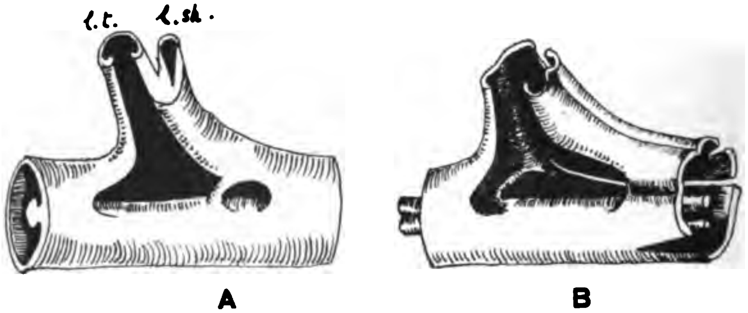

Fig. 58. Evolution of polycycly. A. *Dennstædtia adiantoides*. The internal thickening of the leaf-gap edge can be seen projecting into the pith and continuing into the internode. *l.t.*, leaf-trace; *l.sh.*, lateral shoot.

B. *Dennstædtia rubiginosa*. Two distinct free internal strands can be seen, one connected with the edge of the leaf-gap. After Gwynne-Vaughan.

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[1] Gwynne-Vaughan ('03).

from one to three separate concentric vascular strands present in the pith of the stele, and never coming into connexion with the main cylinder except at the nodes. At each node a single internal strand approaches the free margin of the leaf-gap, and gradually fuses with it, until the two xylems are perfectly continuous, giving an appearance exactly as in *D. adiantoides*. As soon as the leaf-trace has departed the internal strand separates from the cylinder and passes as a free strand into the internode beyond. Distinct protoxylem groups in a mesarch position are found in these internal strands, but they do not appear to be in any way related to those of the leaf-trace.

The frequent development of lateral shoots from the bases of the petiole, with a vascular supply originating from the base of the leaf-trace, may provide, in these plants, the immediate stimulus to the development of the internal strands of the main stele. Separate vascular strands sometimes run from the margin of the leaf-gap, from the point where the vascular cylinder is reinforced by the junction of the internal strand, directly to the tissue supplying the cylinder of the lateral shoot (Fig. 58, A).

A more elaborate system of internal accessory vascular strands is to be met with in *Pteris elata* (Fig. 59), which has an erect or oblique rhizome, with the leaves arranged radially. The vascular system is perfectly solenostelic and the leaf-gap is confined to the base of the trace. The structure of the internal accessory system varies according to the dimensions of the plant, and according to the point at which the section is taken. In a rhizome of average thickness (Fig. 59) the internal system usually consists of a large gutter-shaped strand or of a completely closed cylinder, the latter being generally present for some distance below each node. As the

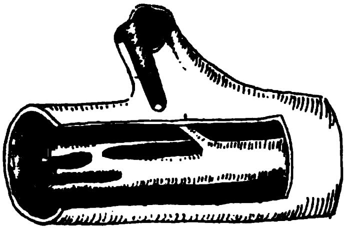

Fig. 59. *Pteris elata* var. *Karsteniana*. An internal accessory perforated cylinder connects by an ascending branch with the edge of the leaf-gap (here confined to the base of the trace). An additional delicate strand is seen inside this cylinder and connected with it just in front of the point of closure of the gap made by the departure of the ascending branch. After Gwynne-Vaughan.

leaf-gap is approached from below a fairly large flat strand is seen to separate from the internal vascular cylinder, and travelling forwards and outwards, fuses completely and finally with the anterior margin of the leaf-gap of the outer cylinder just as the latter closes up. The departure of this flat strand converts the cylinder into a gutter which gradually closes up in the internode above, so that a hollow cylinder is again formed. But sometimes the next gap is formed before the last is closed, so that a dictyostelic structure is produced in the internal cylinder. In large and well-grown rhizomes a second internal vascular cylinder is to be found lying inside the first. It consists simply of a small free rounded strand (Fig. 59), which fuses with the margin of each of the gaps in the internal cylinder, but separates again very soon. In fact it behaves towards the internal cylinder exactly as the internal strand of *D. rubiginosa* behaves towards the primary cylinder. In some cases the connexion of the strand with the internal cylinder is made by means of a branch which terminates at the gap. In rhizomes of medium size the edges of the gaps of the internal cylinder are simply thickened like those of the solenostele of *D. adiantoides*.

In the genus *Matonia* the structure of the vascular system is essentially the same. In *M. sarmentosa* there are two concentric cylinders in the internode; the internal one is sometimes "haplostelic" and sometimes solenostelic. The structure of the node has not been examined, but there can be little doubt that the internal cylinder connects with the outer one either directly or by a branch.

Matonia pectinata. The structure of the complicated vascular system of this Fern is worth describing in some detail, because it has been thoroughly worked out (Tansley and Lulham, '05), not only in the adult rhizome but in the young plant, and the result shows a gradually increasing elaboration of structure, the course of which fully bears out Gwynne-Vaughan's interpretation of the series of cases met with in *Dennstædtia* and in *Pteris elata*. Although the ontogeny of the vascular system of Ferns will be dealt with in a later lecture, it is convenient to consider that of *Matonia pectinata* in connexion with the adult structure.

The stem of *M. pectinata* is a subterranean creeping rhizome with distichous leaves arising in a dorsolateral position. In the large rhizomes of the adult plants, however, the leaf-traces occupy a dorsal position and are practically monostichous.

The stem of the very young plant contains a simple slender protostelic (Fig. 60 A), strand, and the earliest leaf-trace is of exactly the same nature (E). Internal phloem arises before the second trace departs (B) and is formed in connexion with the adaxial phloem of the trace, as in the *Lindsaya*-type. The stele now increases greatly in diameter and isolated endodermal cells appear in the internal

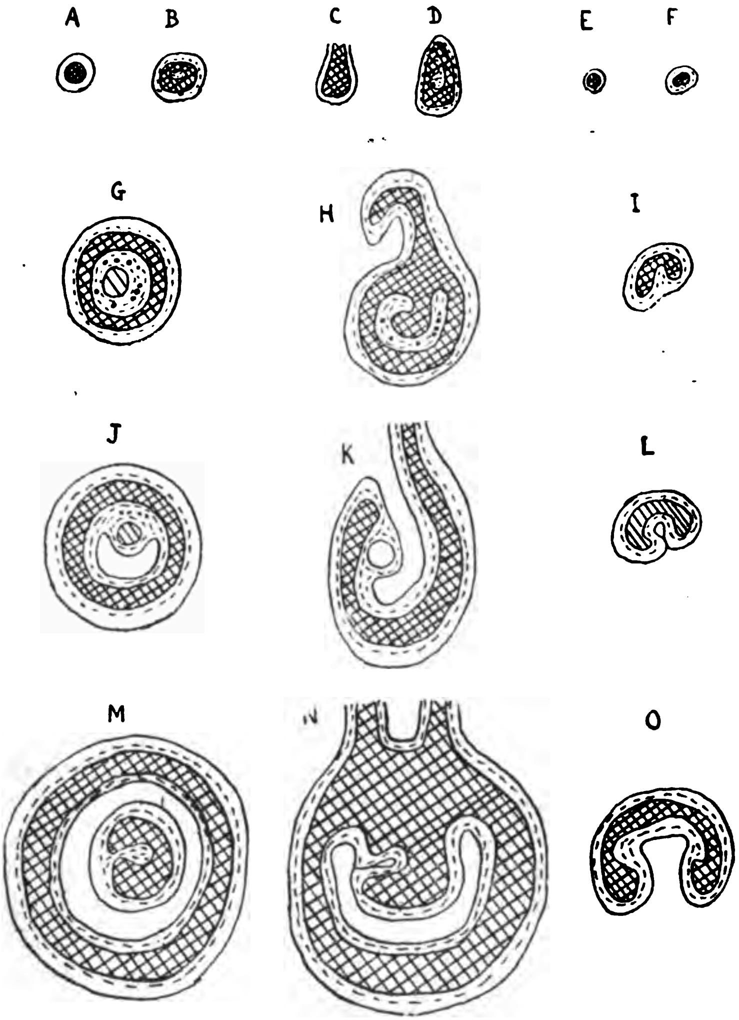

Fig. 60. *Matonia pectinata.* Series of diagrammatic transverse sections drawn to scale to show the increasing complexity of the stelar system in the ontogeny.

The figures in the first column represent the internodal, those in the second column the nodal condition, while those in the third column represent transverse sections of the base of the leaf-trace. For further explanation see text.

phloem (G). These are connected with the adaxial endodermis of the next leaf-trace. During the early stages in the separation of the trace, the internal phloem has a curved cross-section (D), its concavity being occupied by an internal thickening of the xylem, which corresponds with the thickening of the edge of the leaf-gap in *Dennstædtia apiifolia.* In some cases this thickening is continued as an isolated strand of tracheids in the internal phloem (G), and joins the dilatation of the xylem at the base of the next trace Subsequently the internal strand of xylem becomes a constant feature of the stele, usually separated from the main cylinder during the greater part of the internode, but practically always connecting with it at the base of the leaf-trace (H). Tracheæ often run up from the internal strand to the point in the external xylem from which the last tracheids of the trace have departed, but do not contribute to the trace itself. The internal endodermis becomes a continuous strand connected at the nodes with the adaxial endodermis of the leaf-trace, which is now kidney-shaped in cross-section, the endodermis being "invaginated" into the concavity of the trace. Later on a ground-tissue pith appears, both in the leaf-trace (L) and in the stele (J), inside the internal endodermis. These piths are often connected with one another, but neither of them connect, at this stage, with the cortex. When such a connexion first occurs it is the pith at the base of the trace which first opens to the cortex. Later on the stele itself opens in front of the trace, forming a true leaf-gap (K.) Phloem extends from one side into the middle of the internal xylem-strand (M), and now the dorsal half of the strand frequently moves up and helps to close the gap made in the external xylem by the departure of the trace (N). Previously the gap has been closed by the edges of the external xylem approximating as the leaf-trace tracheæ move out. An internal endodermal strand appears in the midst of the internal phloem of what may now be called the second cylinder. By this time the trace has become horse-shoe-shaped in section, with thickened ends (O), or with abaxially directed xylem hooks (Fig. 61, R). At a slightly more advanced stage these hooks are elaborated into free abaxially directed limbs of the trace (S). The hooks or limbs are supplied with tracheæ from the dorsal half of the internal cylinder, which now for the first time directly contributes to the leaf-trace (Q). In the next stage of elaboration the internal cylinder has acquired a pith (T), and regularly opens at the node, sending off a dorsal column of tissue, which fills the leaf-gap in the outer cylinder and also supplies the abaxially directed limbs of the trace on each side (U). Eventually the trace undergoes a final complication, the abaxially directed limbs being again curled inwards, so that their free edges are now directed adaxially (V and Y). To meet this complication the second cylinder now sends up a *double* branch on each side, so that both the limbs of each lateral loop are supplied by the internal cylinder. As the diameter of the whole stele increases the second cylinder, instead of sending up the column of tissue shewn in Fig. 61, U, gradually raises its roof towards the node, so that it comes into bodily contact with, and thus supplies the lateral loops of the leaf-trace on each side, while a tongue of tissue passes forwards and upwards, as in *Pteris elata*, to fill the gap in the outer cylinder. The free edges of the outer limbs of the lateral loop on each side are continued downwards and *forwards* as upstanding flanges (X, *fl*) along the edges of

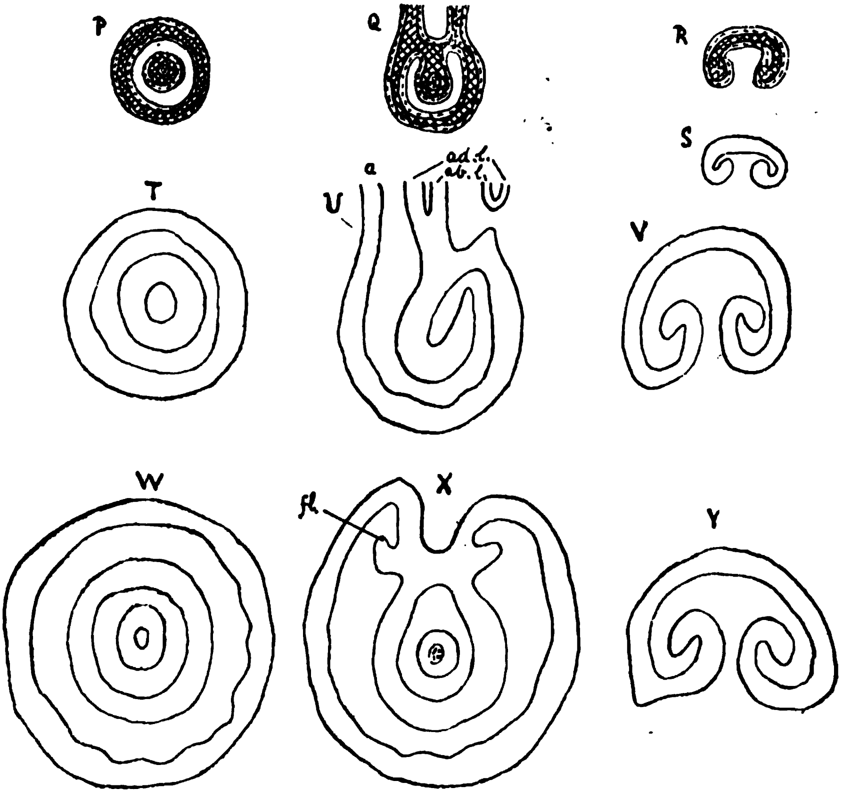

Fig. 61. Continuation of Fig. 60, drawn to a scale one-third that of Fig. 60. In T to Y the outlines only of the vascular cylinders are drawn.

the gap in the second cylinder made by the passing off of the dorsal tongue; so that the final adaxially directed limbs of the lateral loops (the last to appear in evolution) are actually supplied from part of the second cylinder *in front of the base of the trace.* The considerable demands thus made by the trace lead to the appearance of a *third cylinder* (W and X), which arises as an elaboration of the edge of the gap in the second at a point anterior to the dying out of the flanges referred to. This third cylinder, which may be either haplostelic, of *Lindsaya*-type (X) or solenostelic (W), is only found in the largest rhizomes with the largest leaf-traces.[1]

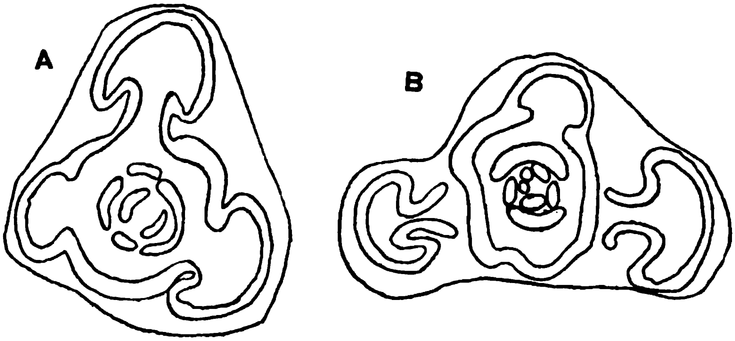

Fig. 62. *Saccoloma adiantoides.* Two diagrammatic transverse sections of the stem showing stages in the detachment of the leaf-traces, and the accessory internal cylinders. In B the beginnings of a fourth system. From Mettenius.

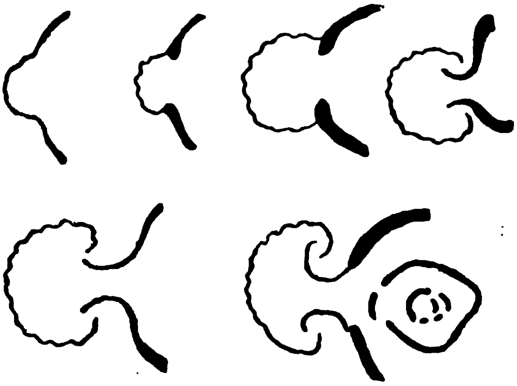

Fig. 63. *Saccoloma adiantoides.* Stages in the formation of a leaf-trace from the external cylinder. In the last figure the detachment of a strand from the second cylinder which will fill the leaf-gap. From Mettenius.

The above summary of the main facts of structure of this complex vascular system clearly shows that it is developed along the lines suggested by Gwynne-Vaughan, and further that each cylinder in turn passes through the *Lindsaya*-phase in progressing from the haplostelic to the solenostelic-type. We also see that the local internal dilatation of the cylinder in the region of the node is, in the first instance, a reinforcement of the water-conducting capacity of the stele immediately in front of the point at which it is diminished by the departure of the leaf-trace. Secondarily the internal strand is drawn into supplying the recently added portions of the elaborated leaf-trace, and in so doing becomes, in the extreme case, taxed to such an extent that a third cylinder is developed to reinforce the second in precisely the same way as the second reinforces the first. If the leaf-trace became more complicated still there is no apparent reason why this process should not be carried even further, and additional internal cylinders be developed.

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[1] For further details and additional figures of the vascular system of *Matonia*, see Tansley and Lulham, '05.

The beginnings of a fourth cylinder are actually formed in *Saccoloma adiantoides* Sw. (*Dicksonia Plumieri* Hk.), so far as can be judged from the account given by Mettenius ('65), though the relations are decidedly different from those obtaining in *Matonia*, owing to the radial arrangement and crowding of the leaves. *Saccoloma* is a big fern with an upright cylindrical stem, 1½″ thick in Mettenius' specimen, and radially arranged leaves showing a divergence of $\frac{8}{21}$. The vascular system (Fig. 62, 63) consists of three concentric cylinders, the outermost of which is broken only at the leaf-gaps, while the second locally breaks into two or more arcs, and the third normally consists of two similar, but of course smaller, arcs.

The leaf-traces are derived entirely from the external cylinder, the gaps created by their departure being filled up by the moving out of arcs from the second cylinder, which in turn is regenerated by the outward passage of strands from the third innermost cylinder. This last is reconstituted by the branching of its strands below the point at which they begin to move out, so that the beginnings of a fourth cylinder are found at certain levels (Fig. 62, B, and Fig. 63, last figure). The inner cylinders in this case are purely compensatory in function, and are not drawn into supplying the leaf-traces directly.

Acrostichum aureum (*Chrysodium vulgare*) is an example of a fern with a simple type of polycyclic stem—the solenostele possessing a few internal, short, irregularly branching and anastomosing, blindly ending accessory strands, one of which fills each leaf-gap (Fig. 64)—but with a very complicated leaf-trace and a great number of petiolar strands. The internal gap-filling strand takes

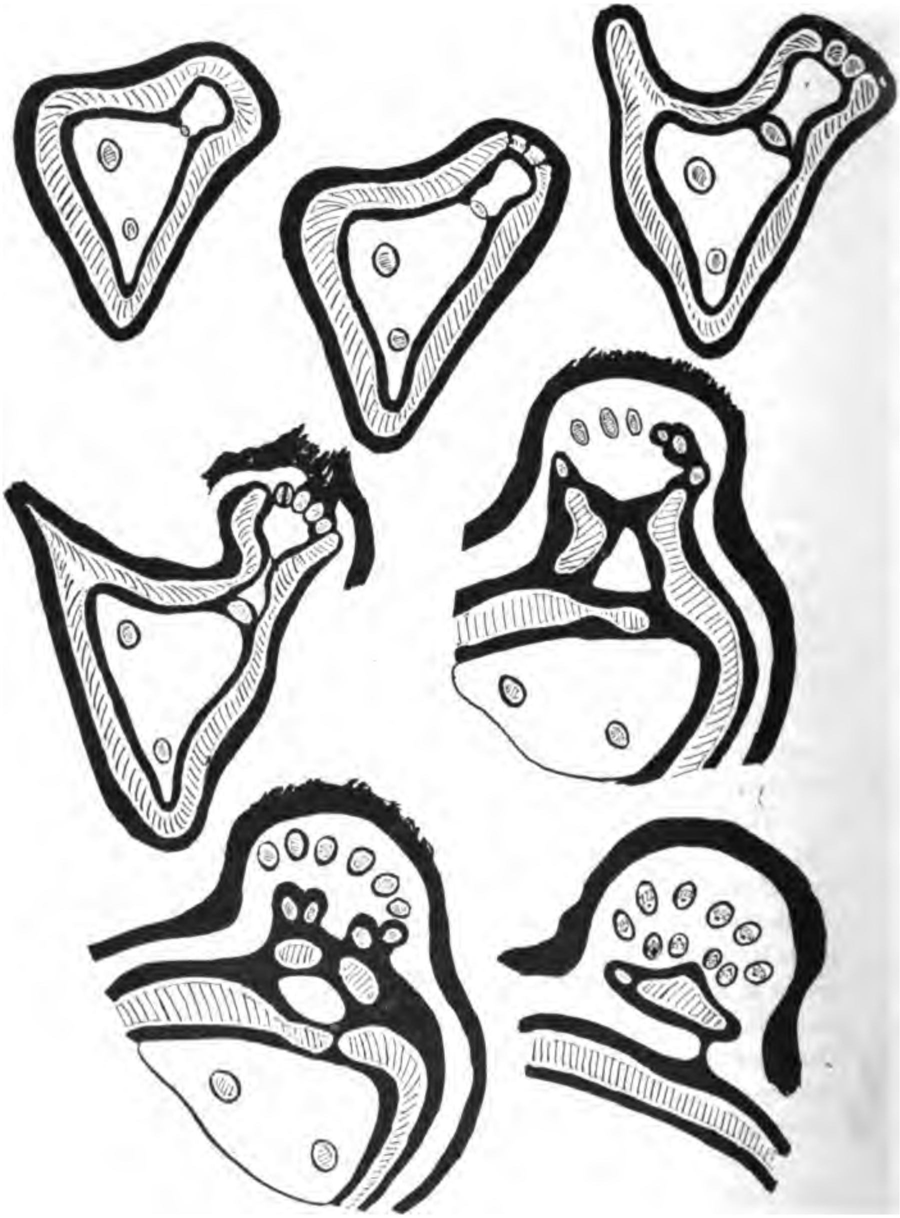

Fig. 64. *Acrostichum aureum.* Series of transverse sections through the node, showing successive stages in the separation of the leaf-trace, and the filling of the leaf-gap by one of the internal accessory strands. From Thomas, '05.

no part in supplying the leaf-trace. The stem and leaf-structures seem rather out of relation, and when the structure of other species of *Acrostichum* is considered it would seem that the leaf-trace must have undergone considerable independent evolution. It is possible also that the cauline vascular system has been reduced from a more complex type. Concerning the possible causes of such phenomena we are unable to say much in the present state of our knowledge.

ON THE DISTRIBUTION OF THE HEPATICÆ, AND ITS SIGNIFICANCE.

By Douglas Houghton Campbell.

(Professor of Botany at Stanford University, California).

THE many important researches on palæozoic and early mesozoic fossils made during the past few years have very much altered the conclusions formerly accepted as to the nature of many fossil plants. While no doubt many of these new conclusions will be accepted, there is no question that some of the recent ones are premature, and are scarcely warranted by the evidence at hand; so that it will perhaps be just as well to pause before throwing over without question the results of work done in other lines than those of palæontology.

In his admirable survey of the present position of palæozoic botany (Progressus Rei Botanicæ: June, 1906) Dr. D. H. Scott, in commenting on the great scarcity of unmistakable bryophytic remains in palæozoic formations, while admitting that too much stress should not be laid upon negative evidence, nevertheless is evidently inclined to the opinion that the evidence at hand indicates that the Hepaticæ are not improbably of comparatively late origin.

As one of the botanists who believe that the Hepaticæ form a very important link in the evolutionary series leading up to the higher plants and are really ancient types, the writer has thought it worth while to call attention to certain facts that have not received much attention, and that may have a bearing upon the question of the antiquity of the Bryophytes.

The presence of impressions from palæozoic rocks, which there seems no good reason to doubt belong to genuine Marchantiaceæ, are cited by Dr. Scott; and of the mosses the fossil *Muscites polytrichaceus*, Renault and Zeiller, seems to be generally admitted to be a true moss. Both of these belong to the more specialized types, and admitting that they are correctly identified, they must have been preceded by a long series of simpler forms.

While it is true that very delicate tissues have been preserved in a fossil condition in some Pteridophytes, in most cases, at least, these are protected by a covering of more resistant tissues, as in the delicate parenchyma of stems, or the tissues within sporangia and seeds. The hyphæ of Fungi, also, that are known in a fossil condition, are protected within the tissues of other plants. The tissues of all Hepaticæ are excessively delicate and perishable, and the resistant parts such as the elaters are of microscopic dimensions and would certainly be overlooked unless very careful search was made for them. It may very well be that a rigid examination of sections of the masses of petrified material might reveal traces of elaters; or evidences of epiphyllous species, such as are so common at present in wet tropical forests, might reward a careful study of the surface of the fern leaves that are so abundant in the palæozoic rocks.

It is not strange that the study of the vascular plants has largely monopolized the attention of students of palæozoic botany; but until one can be sure that the same exhaustive methods have been used in the search for bryophytic remains that have characterized the study of the vascular plants, one may be pardoned for maintaining a somewhat sceptical attitude in regard to the assumed unimportance of Bryophytes in the palæozoic flora.

The remains of Bryophytes are almost as scarce in the later formations, except for the interesting forms found in amber (Engler and Prantl—1 Th., 3 Abt., p. 134.) The latter are too recent to throw much light on the question, and are all very close to living genera.

It must be admitted, then, that our present knowledge of the fossil

Bryophytes is too scanty to be of much value in determining the geological history of the group, although what little evidence is available is entirely in harmony with the assumption of their primitive character. The arguments based upon comparative morphology are sufficiently familiar and have been recently summarized by the writer (Mosses and Ferns—2nd Edition, Chap. XV.); they need not be repeated here. There is, however, a point that has not been considered as fully as it might have been, and the present paper is an attempt to present this, since it seems to throw a great deal of light upon the subject of the antiquity of the Bryophytes. The point in question is the present geographical distribution of the Bryophytes, especially of the Hepaticæ.

That a study of the present distribution of any group of organisms is one of the most important means of determining their relative antiquity is generally recognized. Of course there are many factors to be considered, and great care must be exercised before it is safe to make wide generalizations. Most important of all, perhaps, especially in dealing with very wide-spread forms, is the question of the means of distribution in very recent times, and especially the part that man has played, voluntarily or otherwise, in the distribution of many species.

Studies on geographical distribution have concerned themselves largely with the vascular plants, and there are not many critical studies of the distribution of Thallophytes and Bryophytes. It has been generally assumed that most of these forms are old types, and their wide distribution has been accepted as a matter of course. It has also been rather taken for granted that the lightness and small size of the spores of the Bryophytes and Pteridophytes make the rapid dissimination of these plants an easy matter. This latter point; however, will be found not to apply to many of the Liverworts, whose spores are frequently adapted to immediate germination and are not fitted to survive a long journey. Hence the wide distribution of many Hepaticæ must be explained on other grounds than that of rapid distribution by means of the spores.

Although practically nothing is known of the early geological history of the simpler green Algæ, it is very generally agreed that they are very ancient forms. The cosmopolitan character of most genera and of many species point to this, even if the evidence furnished by comparative morphology were ignored. The positive evidence that forms closely allied to many living calcareous Siphoneæ lived in early palæozoic times, makes it extremely probable that the absence from the early rocks of the green Algæ which have no calcareous skeleton is due to the extremely perishable tissues of these delicate organisms.

The distribution of the vascular plants has, of course, received much attention, but it may be worth while to call attention to some of the conclusions that have been drawn from a study of the distribution of the existing Pteridophytes and Spermatophytes, and their bearing upon the deductions to be drawn from a study of the distribution of the Bryophytes. Many of the living genera of both Pteridophytes and Gymnosperms occur in a fossil condition, and together with their present distribution furnish pretty complete data for a study of their geological history.

The distribution of the Angiosperms of the present day, together with what is known of their distribution in the late Cretaceous and Tertiary, when many existing genera were already differentiated, throws a good deal of light upon the history of the group, although it must be remembered that the fossil record is much less satisfactory than is the case with the lower vascular plants. This is no doubt largely due to the much greater proportion of herbaceous species, which were poorly fitted to leave recognizable fossil remains. Many types, which there is good reason to suppose are old ones, are quite unknown in a fossil condition.

At the present day there is a nearly uniform sub-polar zone of vegetation in which the predominant types, *e.g.*, willows, poplars, firs, buttercups, vacciniums, etc., probably represent the descendants, but little changed, of the northern glacial flora. Many of these, like the Amentaceæ and Ranunculaceæ, there is good reason to suppose are among the more primitive angiospermous types. The uniformity in the conditions of this sub-polar zone, as well as its practically unbroken extent, readily explain the very slight variation in the vegetation of such widely separated countries as Scandinavia and Northern Canada.

Proceeding southward, as might be expected, factors come into play that tend towards greater diversity in the flora. The great barriers of mountain and ocean, and the greater range of climatic conditions due to these and other factors, have had their effect. While many of the old tertiary types have survived, undoubtedly many new forms have developed, and others have been more or less completely destroyed through changes in climate, or from causes not so evident.

The very valuable studies of Asa Gray (see Scientific Papers of

Asa Gray, edited by C. S. Sargent, 1889) on the correspondence between the floras of Pacific Asia and Atlantic North America, show the survival in these widely separated regions of many widespread Tertiary genera that have quite disappeared from Europe and from Western America, where there is positive evidence that they once abounded. While the fossil evidence in this case is confined to woody trees and shrubs like Liriodendron, Magnolia and Hamamelis, it is reasonably certain that other peculiar genera, like Podophyllum, Mitchella, Diphylleia, and Nelumbium, are of equal antiquity, and were probably as widely spread as the trees and shrubs associated with them at the present day. The absence of these more delicate plants in a fossil condition must be borne in mind in dealing with the question of the Hepaticæ, which are very much more delicate and perishable than any of these herbaceous angiosperms, and consequently even less likely to leave fossil traces.

The diversity of species grows more marked in the tropical regions, and the number of genera and species common to the tropics of the Old and New Worlds is relatively small. The widespread genera, like Euphorbia, Ipomoea, Solanum, Polypodium, are mostly extratropical as well. The number of strictly tropical genera, common to both hemispheres, is very small.

The very wide-spread genera, *e.g.*, Ranunculus, Ficus, Senecio, are either members of families generally recognized as primitive ones, or else, as in the case of Senecio, are exceptionally adapted to rapid dispersal. It is undoubtedly the latter trait that explains the extraordinary predominance of Compositæ in the modern flora.

We may safely conclude that many existing families and genera of Angiosperms were already differentiated in Tertiary times and have come down to the present with little change. Many genera, however, and probably most existing species, are of more recent origin, and the changes have naturally been most rapid in the warmer parts of the world. The present distribution of most of the highly specialized types, like most Orchidaceæ, Zingiberaceæ, Bromeliaceæ, etc., indicates that these are of relatively late origin, and are not closely allied to the more primitive types of Angiosperms.

The Hepaticæ, including the Anthocerotaceæ, comprise, according to Schiffner (Engler and Prantl, Nat. Pflanzenfamilien I Th., 3 Abt., p. 141) not quite 4,000 species, Since the date of this enumeration (1895) the number has been considerably augmented, but even at the present time the described species can hardly exceed 5,000, or less than half as many as those of the single angiospermous family, the Compositæ. The 3,862 species of true Hepaticæ enumerated by Schiffner, are very unequally divided between the Jungermanniales and Marchantiales, the latter comprising but 275 species, of which more than 100 belong to the single genus, Riccia. Of the Jungermanniales, but 264 belong to the thallose forms or Anacrogynæ, the leafy acrogynous species numbering more than 3,300. To the Anthocerotaceæ are assigned 103 species.

Most of the genera, especially those of the three smaller groups of the Liverworts, are widely distributed, and many genera and a good many species are cosmopolitan. Of the larger cosmopolitan genera, Riccia, Marchantia, Aneura, and Frullania are examples. Other cosmopolitan genera have few species, and are usually less uniformly distributed. Reboulia and Ricciocarpus are examples of such genera among the Marchantiaceæ, and Metzgeria, Pallavicinia and Fossombronia of the thallose Jungermanniaceæ. Some of the larger genera of the foliose Jungermanniaceæ outnumber in species the whole of the Marchantiales, or the thallose Jungermanniaceæ. Thus Frullania is credited by Schiffner with 310 species, Plagiochila with 463.

The smaller genera are usually somewhat discontinuous in their distribution, although they may occur in all quarters of the earth. Thus Targionia, with but two species, is represented in Southern and Western Europe, Africa, Java, Australia and Western America, but is quite absent from Eastern America and from most of Asia. The monotypic *Lunularia cruciata* has a similar distribution in the Old World, but is as yet unknown, except where introduced, in America. Of the anacrogynous Jungermanniales, *Blasia pusilla*, also a monotypic species, is wide-spread through Europe and North America and also occurs in Australia, while Pellia is common to the greater part of the Northern hemisphere. Pellia is not yet reported from the Southern hemisphere, and Fegatella, another widely distributed northern genus, is not yet known south of the equator. Of exclusively southern genera may be cited Funicularia (Brazil), Hymenophyton (South America, Australasia), Zoopsis (Java, Australasia, South America). The genus Calycularia has a rather peculiar distribution. Of the three species, two are tropical—one in Java, one in the mountains of the East Indies—while the third occurs in Arctic Siberia. Monoclea, with two species, is distributed between tropical America and New Zealand. Dumortiera and Dendroceros are widely distributed throughout the tropics, and the former extends beyond the tropics into the warm temperate zone.

Only a small number of species are of limited range, and these are often monotypic. Of these monotypic forms *Wiesnerella Javanica*, Schiff. is as yet known only from Mount Gedeh in Java, and *Geothallus tuberosus* Campbell, has only been collected near San Diego in Southern California. It is not safe to assume that these species are really as restricted in their range as they now appear to be. It is highly probable that they will be found at other places, as has been the case with *Treubia insignis*, which for a long time was known only from Mount Gedeh in Java, but has since been found by its discoverer, Goebel, in New Zealand. A similar case is that of the genus Riella, which until recently was known only from Southern Europe and Northern Africa, but which is now known to occur in Turkestan, the Canary Islands, and in at least two localites in the United States. (Howe & Underwood, The Genus Riella, etc., Bull. Torrey Bot. Club, 30: p. 214, 1903).

The most obvious fact that presents itself from a study of the distribution of the Hepaticæ is the small number of genera and their wide distribution, this being especially the case among those forms which for other reasons are supposed to be the most ancient. The great preponderance of the foliose Jungermanniales is entirely in harmony with the conclusion of the morphologists that they are the most modern of the Liverworts. It is inconceivable that a recently developed group of plants could have spread over the world as the simpler types of Hepaticæ have done, with so little modification, unless there were some extraordinary means of rapid dissemination. There certainly is very little evidence that this is the case with the Hepaticæ. Let us consider the little group of the Anacrogynæ, or thallose Jungermanniaceæ. This group comprises less than 300 species, distributed among about twenty genera. Of the latter, more than three-fourths are either cosmopolitan, or at any rate of very wide distribution. It is only necessary to contrast these figures with those of such an evidently modern group of plants as the family Orchidaceæ, or Compositæ. Out of over 400 genera and 5,000—10,000 species of the former family, probably not a single one is cosmopolitan, and the great majority, both of genera and species, are of comparatively narrow range.

A number of families of Angiosperms, which to judge from their present distribution, must be relatively old ones, have left few or no fossil traces. The Violaceæ and Begoniaceæ may be mentioned as examples of such families. The genus Begonia is widespread throughout the tropics, and extends little, if at all, beyond them. Absolutely no fossil remains of either the extremely characteristic leaves or fruits are known. As these plants occur where one would expect that they might be preserved fossil, the only explanation to be offered of their absence in a fossil state is that their tissues are too delicate and perishable to have left any traces. (See Warburg, Begoniaceæ, Engler and Prantl, III. Th. 6a Abt., p. 133). As no Liverworts approach in robustness most species of Begonia, it is quite as reasonable also to explain their great scarcity in a fossil condition as the result of their extremely perishable nature.

As a rule, the Hepaticæ are not especially adaptable plants. Growing usually in moist shady places, they are not fitted to traverse extended dry or exposed areas. It is commonly assumed that their light spores are fitted for rapid dispersal by wind, but in many of them—and these including some of the most widely distributed genera—the spores have very delicate thin walls and contain chlorophyll, showing that they are adapted only to immediate germination; such spores very soon lose their power of germination. Unfortunately very few data are available on this point, but some experiments made by Mr. H. B. Humphrey, under the writer's direction, showed that none of the spores of this type that were examined retained their vitality more than a few weeks, and in the widespread *Fegatella conica* a very few days' drying quite killed all of the spores. It is highly probable that further experiments on the germination of the spores of most species growing in the wet tropical forests will show that the spores very soon lose their power of germination, and will not survive any prolonged dessication.

It is true that such xerophilous species as *Targionia hypophylla* and *Fimbriaria Californica* have spores fitted to survive long periods of drought, but these are, with little question, secondary forms adapted to a special environment. Some of these xerophytic forms show other modifications due to their peculiar environment. The characteristic tubers of Geothallus and of some species of Fossombronia, are adaptations to extreme xerophytic conditions.

We can hardly explain the present distribution of such widespread tropical genera as Dendroceros, Monoclea, and Dumortiera by the theory that their spores could be carried across the wide ocean barriers that separate the regions where they now occur, as the spores are not of the type that could be carried long distances without perishing. Since there are no connecting forms in the higher latitudes that could explain the passage of these forms from one tropical zone to the other, we can only assume that these genera are the little changed descendants of ancient widely distributed types.

The ready distribution of Ferns, by means of their spores, has often been cited, but with these, as with Hepaticæ, there are great differences as to the ease of distribution. Ferns with thick-walled colourless spores are readily disseminated, as the spores retain their power of germination for many months, or even years. But there are other ferns, such as the Hymenophyllaceæ and Osmunda, whose spores quickly perish unless they immediately have the conditions necessary for germination. We know, however, from the fossil record, that both the Hymenophyllaceæ and Osmundaceæ are old types, and their present wide distribution is readily accounted for by this assumption. These ferns may very well be compared with the Hepaticæ of wide distribution whose spores are not fitted for extended dissemination.

An admirable opportunity for studying on a large scale the relative adaptability of plants for rapid distribution, has been offered by the island of Krakatau, which, as is well known, was practically entirely denuded of all vegetation by the great eruption of 1883. Since that time a number of visits have been made from Buitenzorg to the island, and the gradual re-establishment of the vegetation has been carefully noted. Last year (April, 1906), the writer had an opportunity of visiting Krakatau, and observing the present condition of the vegetation. The island is now quite covered with plants, including many trees of considerable size. Owing to the limited time at our disposal and the difficulties of cutting a way through the dense growth of tall grasses that cover most of the lower land between the shore and the central volcanic cone of the island, our observations were necessarily confined to the region near the shore, where there is a narrow belt of woods. When the island was first visited about three years after the eruption (Treub, Ann. du Jardin botanique de Buitenzorg, VII., 1888), eleven species of ferns had already established themselves, as well as a number of flowering plants with easily carried seeds and fruits, such as several grasses and Compositæ. At the present time several species of Orchids are abundant, as well as many grasses

Ferns, and most of the characteristic shore plants of the Eastern Tropics, *e.g.*, Cocoa-nuts, *Ipomoea pes-caprae*, Casuarina, etc.; but as yet very few mosses have been found (Treub reported two undetermined species), and no Liverworts have been collected. It is not unlikely, when a careful search has been made in the central part of the island, where a forest growth has begun to develop, that some Hepaticæ will be found; but in a day's collecting, keeping a special look-out for Hepaticæ, the writer was unable to find a single specimen, and as we have already stated, none have been reported by other collectors.

Inasmuch as Krakatau is within sight of Java and Sumatra, both of which have an extremely rich hepatic flora, the absence of these plants from the new flora of Krakatau is, to say the least, worthy of note.

We may justly conclude then, that the distribution of the existing Liverworts indicates that they are ancient forms whose scarcity in a fossil condition is due to their very perishable tissues. It may be reasonably expected that a more rigid examination of the palæozoic fossils by modern methods will add materially to the small number of fossils that have already been referred to the Bryophytes.

While the Mosses are presumably a more recent and specialized group than Hepaticæ, still their distribution indicates that they also must have been differentiated at a very early period. Such a genus as Sphagnum, for example, absolutely cosmopolitan, and yet peculiarly unfitted for rapid distribution, must be a very old type.

THE MEETING OF THE BRITISH ASSOCIATION AT LEICESTER.

THE Leicester meeting (July 31st—August 7th) was not a large one, but much good work was done in the Section Rooms, and the local arrangements were rather exceptionally good.

Section K met under the presidency of Professor Farmer, who delivered an able and incisive address, calling attention to the prospects which are opening up of explaining vital phenomena in terms of chemistry and physics. His strictures on those who would "explain the appearance of a structure on the ground of its utility" were severe. He stigmatised such supposed "explanations" as "both superficial and unscientific" and complained that they tend to "bar the way of enquiry just where scientific investigation ought to commence," this investigation consisting, of course, in the constant attempt "to analyse our problems, as far as may be possible, into their chemical and physical components." The rest of the address consisted of a very suggestive and interesting, though necessarily condensed, consideration of the present condition and future possibilities of such analysis in regard to very various phenomena, such as the alternation of reproductive and vegetative phases in certain Fungi, the phenomena of nuclear division, of heredity, and of gall-formation. If we might venture a word of criticism, it would be that the President's remarks are likely to be thrown away upon those, if such there be, who really believe that the usefulness of a structure or process is a complete explanation of its appearance. Such a belief can only exist in the absence of the most elementary appreciation of the aims and methods of science. At the same time it is scarcely necessary to point out that usefulness is often, though not always, a condition of survival, and therefore, in so far, a partial explanation of persistence. The failure to get behind the teleological "bar" may be due to want of energy or capacity in the investigator, or to the inherent difficulty of the further analysis of the phenomena with which he is dealing, but scarcely to a wrong philosophical conception, since the logical problem presented is of the simplest kind.

A large part of the time of the section was occupied in joint meetings with other sections. Thus there was a joint meeting with Zoology, Geology, and Geography, to hear Professor Conwentz, the Prussian State Commissioner for the Care of Natural Monuments (Naturdenkmalpflege). Professor Conwentz' address (of which some account will be found in *Nature*, September 26th,[1] "Botany at the British Association",) should be very useful in directing attention to the importance of preserving carefully selected samples of characteristic scenery and primitive or semi-primitive vegetation from the attacks of building, cultivation, etc. Such an address has a two-fold appeal—scientific and æsthetic. What has been done hitherto in this country has been almost confined to the latter aspect, that is to say the efforts that have been made to preserve scenery have been directed by a desire to prevent the piece-meal destruction of the beauty of our native land. The former aspect, which has been recently brought into fresh notice by the creation of such bodies as the Central Committee on British Vegetation, should have new emphasis given to it by Professor Conwentz' prozelytizing efforts, which have had such remarkable success in Germany. During the short time he has been in a position to give official weight to his work in this direction, most gratifying practical results have been achieved. We understand that Professor Conwentz proposes to publish a volume on the subject in English. The question of the best means of practical action in this country remains to be settled.

A joint meeting with the Zoologists to discuss the Physical Basis of Inheritance, a discussion opened by Professor Hickson, will be found reported in "Zoology at the British Association" (*Nature*, September 19th). The weight of the evidence, developed by the various speakers, both from cytology and from the facts of heredity, leads to the conclusion that the material of the chromosomes is of primary importance in hereditary transmission, though, as was pointed out in the discussion, the chromomeres contained by the chromosomes are more likely to correspond with the "primordia" of somatic characters than the chromosomes themselves, and if these promordia are to be regarded as the architects of the body, yet the nature of the material with which they build, *i.e.*, the cytoplasm, necessarily has an effect upon the nature of the finished structure.

A joint meeting with the Zoologists and Educationists was held to discuss the "Teaching of Biology in Schools." Attention may be called to the views of Mr. O. H. Latter, who opened the discussion, as to the best biological curriculum for school children. Mr. Latter advocated nature-study methods for the lower classes in a school, and an avoidance of the type system. The theory of evolution, without which the ordinary type system is meaningless, is, he thinks, beyond the grasp of any but the most advanced pupils. When "nature-study" has done its work, an interval of chemistry and physics might be interpolated to lead on to physiological work, as the mind of the growing child naturally desires to penetrate beyond the surface phenomena to problems of causation.

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[1] A fairly full account will be found of most of the papers read at the Meeting in this article, to which we refer our readers. In the present notice we shall confine ourselves to commenting upon the papers and discussions.

Of purely botanical discussions the longest was that on the Cytology of Reproduction in the Higher Fungi; of which a fairly full account is given in the article already referred to. Here we need only to congratulate Miss Fraser and her colleagues and pupils on being so successfully engaged in developing a difficult and fascinating part of cytological investigation, and Professor V. H. Blackman, to whom the original inspiration is due, on having founded a flourishing little "school" of cyto-mycological research.

PHYSIOLOGICAL PAPERS.

Professor Armstrong's paper (in conjunction with his son, Dr. E. F. Armstrong) on "Enzymes, their Mode of Action and Function," was one of the most deeply interesting contributions to the Sectional proceedings. Professor Armstrong brought very vividly before botanists the immense interest and importance of the work that is now being done on the action of enzymes in living beings. The outstanding modern conclusion of the reversibility of all enzyme action has led on to the belief that not only destructive but constructive metabolic changes are under the control of these bodies, and that this is the great characteristic of chemical changes going on in the living body. The conception of an enzyme as a skeleton into which the groups of atoms that go to make up the structure of the most complicated organic bodies can be packed enables us to see how the conception of the mechanism of anabolism can be simplified. The complete paper will, we understand, shortly appear in the *Annals of Botany*.

Professor Bottomley's success in greatly increasing tomato crops by the inoculation of nitrogen-fixing bacteria previously cultivated in tomato juice, and in inducing the bacteria to live in the cortex of the roots of wheat-plants is of obviously great importance both scientifically and economically.

MORPHOLOGICAL PAPERS.

The main result of Professor Bower's account of his comparative work on the Embryos of Pteridophytes was the conclusion that the principal organs of the plant are not laid down, as Goebel supposes, entirely on a basis of "physiological opportunism," but that the main axis of polarity is determined by the formation of the first segmentation, the centre of the epibasal segment corresponding with the stem apex. On the other hand, the relation of the polarity of the embryo to the axis of archegonium is quite variable, and so is the number and position of the first leaves and roots. Professor Bower was very successful in bringing into line with his general view a number of apparently anomalous cases.

The sensation of the meeting from the anatomists' point of view was the demonstration by Mr. Gwynne-Vaughan that the "tracheids" of Osmundaceæ and many other Ferns are in reality not tracheids at all, but a peculiar type of vessel in which the pits are open perforations, and are also in free communication, one with another, in the thickness of the wall, by the disappearance of the middle lamella, so that the walls of the xylem elements are really skeletons built up of corner columns joined by horizontally running pairs of bars. It is not, perhaps, altogether creditable to fern-anatomists that they have so long missed this elementary fact of structure, which can be very readily demonstrated.

Professor Oliver read an interesting description and discussion of Williamson's palæozoic seed *Physostoma elegans*, nearly related to Lagenostoma. He regarded it as being one of the most primitive types of Pteridosperms yet discovered.

Mr. D. M. S. Watson described the cone of *Bothrodendron* (*Lepidodendron*) *mundum* as practically a Lepidostrobus with the radial extension of the sporophylls very much reduced, a state of things we should expect from a consideration of the vegetative organs.

ECOLOGICAL PAPERS.

Professor H. H. W. Pearson's paper describing his excursion to the "Welwitschia-desert" in German S.W. Africa was of great interest. This is of course the first thorough account we have had of this interesting plant in its native home. Two of the most interesting points brought out are the pollination of Welwitschia by a hemipterous insect and the inference from the non-occurrence of young plants in Damaraland that the conditions of germination must occur very rarely, and hence that the species is probably doomed to extinction in its native habitat. Germination occurs readily enough under proper conditions, as is evident from the raising of numerous seedlings in this country from seeds sent home by Professor Pearson.

Professor Yapp communicated some of the first results of his systematic study of the Ecology of Wicken Fen, showing that the distribution of hairiness of the leaves in the meadowsweet is correlated with the need of protection against over-transpiration both seasonally and also on each individual leaf.

Mr. William Bell, the local Secretary of the section, read a paper on Charnwood Forest, illustrated by particularly beautiful lantern slides, in which, after a general description of the Forest, he traced the progress of enclosure and disforestation, and by comparison of early eighteenth century lists with present day records reached the result that while many bog and water plants have greatly lessened in numbers, and in some cases become extinct, woodland plants have decreased to a less extent, and pasture and arable plants have greatly increased.

There was an excellent excursion to the Forest on Saturday, organised by Mr. Bell. In the course of some fourteen miles walk the members of the section visited Bardon Hill, Beacon Hill, Bradgate, and Groby Pool, and got a very good idea of the characteristic vegetation of several parts of the Forest still bearing woodland. The general type on the hills mentioned is the dry oak-wood with much Birch; *Aira flexuosa* and associated plants form the undergrowth of the higher slopes, while *Holcus mollis* and *Scilla* are dominant at lower levels.

Mendelism was represented by a paper read by Mr. Gregory on the inheritance of certain characters in *Primula sinensis*, which served to illustrate the complications of the simple Mendelian rules with which workers now have to deal. An excursion to Burbage to inspect Mr. C. C. Hurst's Mendelian experiments was also a prominent feature of the programme.

Professor Weiss gave the semi-popular lecture, and dealt with some of the newer work on pollination.

Mr. William Bell looked after the local arrangements with the greatest assiduity and devotion to detail and his care secured very smooth working of everything upon which the comfort of Section K depended.

BOTANICAL APPOINTMENTS.

Mr. A. A. Lawson, lately Assistant Professor of Botany at Stanford University, California, has succeeded Mr. Gwynne-Vaughan as Senior Assistant in Botany at Glasgow University.

Mr. R. P. Gregory (St. John's College) has been appointed University Lecturer in Botany at Cambridge, in succession to Mr. A. W. Hill, who recently became Assistant Director of the Royal Gardens, Kew. Mr. A. M. Smith (Emmanuel College) takes Mr. Gregory's place as Senior University Demonstrator in Botany.

Dr. Percy Groom has been appointed Lecturer in Botany at the North London Polytechnic in succession to Dr. S. E. Chandler.

* * *

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UNIVERSITY LECTURER IN BOTANY, CAMBRIDGE.

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LECTURES ON THE EVOLUTION OF THE FILICINEAN VASCULAR SYSTEM.[1]

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LECTURE VII.

POLYCYCLY—*continued.*

[FIGS. 65—80.]

IN *Pteris incisa* var. *integrifolia,* and in *Pteris aquilina* we have a type of polycycly distinctly different from those we have hitherto been considering, for here the supply of part of the leaf-trace is the most important function of the internal accessory vascular system.

Pteris incisa Thunb., according to Gwynne-Vaughan ('03), is a typical solenostelic fern, with a leaf-trace rather of the *Hypolepis*-type. In the variety *integrifolia* there has been found[2] a curious complication probably connected with an increase in the elaboration of the frond. In the specimen examined (Figs. 65 and 66) each leaf arises in the angle between the two branches of a stem-dichotomy, the branches being so small relatively to the petiole that their steles arise by constriction from the sides of the leaf-trace, which forms the direct continuation of the vascular system of the main stem. The stele of the main stem (the diameter of which is about double that of Gwynne-Vaughan's type) is a typical solenostele with a deeply waved outline. As the node is approached internal folds (Figs. 65 and 66, A and B) arise from the inner wall of the vascular ring, one on each side of the stele. The whole structure increases greatly in size and the internal folds open to the cortex through the wall of the stele. At the same time the dorsal wall of the stele breaks in the middle line, so that the whole vascular system acquires the general form of a leaf-trace with deep inward folds A′ and B′) on the two flanks. The two branch steles of the dichotomy are now separated off to the right and to the left from the dorsal half of the trace, but they are contributed to by hollow cylindrical strands arising from the ventral half (*e*, etc., Fig. 66).

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[1] A Course of Advanced Lectures in Botany given for the University of London at University College in the Lent Term, 1907.

[2] Tansley and Lulham ('04).

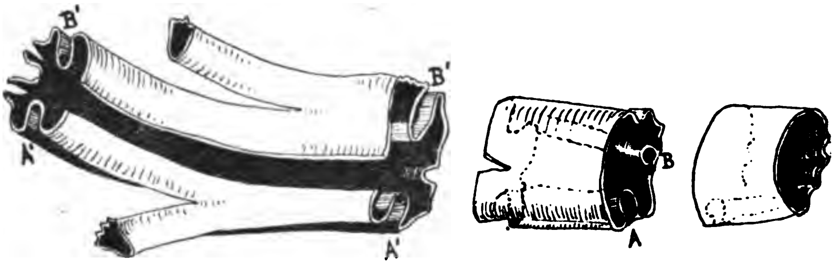

Fig. 65. *Pteris incisa* var. *integrifolia*. Vascular system of node seen from dorsal side. The stele below the node is seen in sections, the parts between cut away. A, B, lateral folds of solenostele, A′, B′, of leaf-trace. From Tansley & Lulham.

The result is that the extended flanks of the trace are considerably abbreviated, though the whole remains of the same general form, which is that of the *Hypolepis*-type but considerably more folded. The two conspicuously deep lateral folds (A′ — B′) are continuous below with the internal folds (A, B) of the solenostele already described. Since these folds gradually die out in the internode below there can be little doubt that they represent a decurrent development of the lateral folds of the leaf-trace. Part of the wall of each branch-stele (*black* in Fig. 66) is also continuous with the corresponding fold of the main solenostele, and this is connected with the absence of gaps, such as are found in *Hypolepis*, at their bases (see Gwynne-Vaughan, '03, Plate 33, Figs. 5, 6).

Pteris aquilina (Fig. 67) has, strictly speaking, a dissected dorsiventral solenostele on the definition adopted in these lectures, since the *leaf-gaps* are comparatively remote, and do not overlap, though there are numerous other gaps which do. The petiolar system, as is well-known, consists of a number of separate strands, the arrangement of which eventually becomes very confused. At the base, however, the outline of the leaf-trace as a whole is of exactly the same type as in the plant just described. The deep lateral folds of the trace are here also exclusively supplied by the internal vascular strands of the stem, which take the well known form of two slightly curved vascular plates within the inner sclerenchymatous ring. Branches from both dorsal and ventral strands of this system pass up into the petiole and form the lateral folds of the petiolar system. In this case we must suppose that decurrent strands from these folds have extended throughout the internode and become a continuous internal vascular system. It is of interest to note that here again a compensation-strand (*c.s.* Fig 67) arises from the internal system and helps to repair the short leaf-gap in front of the origin of the trace. Thus in both these species

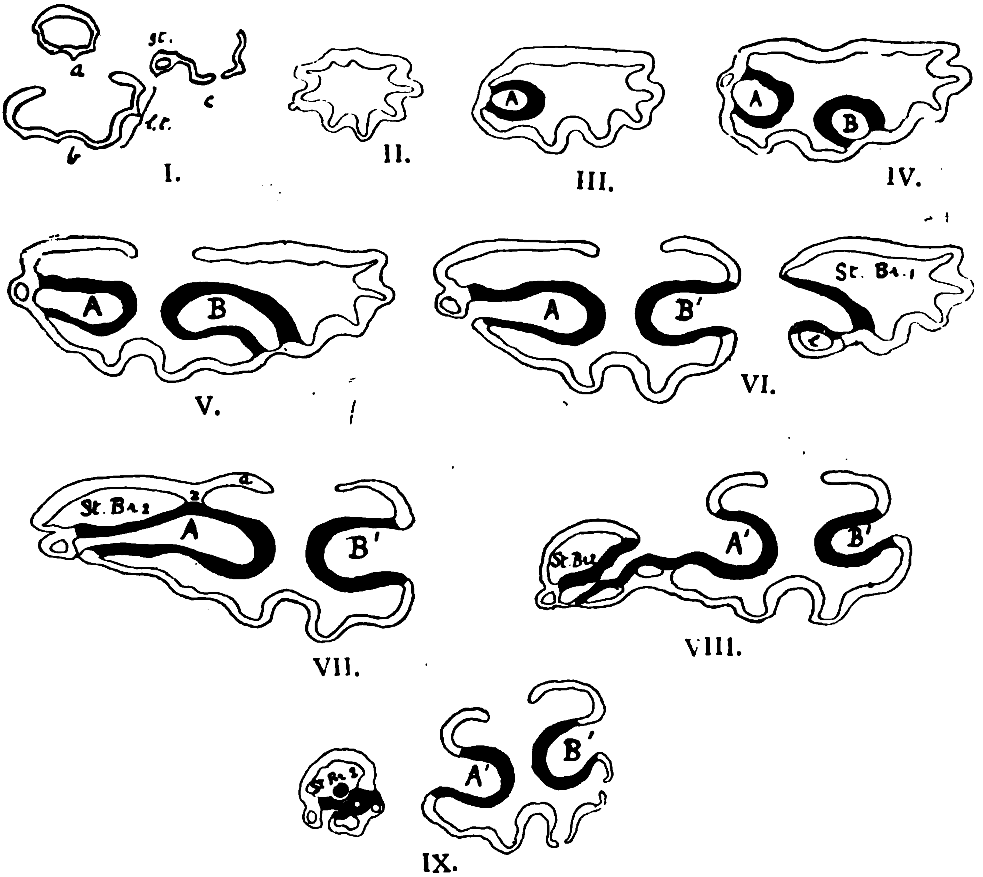

Fig. 66. *Pteris incisa*, transverse sections. (all × 6). I.—*Pteris incisa*, type (from Gwynne-Vaughan's preparations). *a.*, stele of internode. *b.*, separation of leaf-trace. (*l.t.*) *c.*, separation of branch stele (*st.*), from base of petiolar strand (of *Hypolepis*-type). *Pteris incisa* var *integrifolia*. II.—Stele of internode. III., IV.—Origin of lateral folds (A, B.) V., VI.—Separation of first branch-stele and opening of folds. VII.—IX.—Separation of second branch stele, leaving petiolar strand of deeply folded *Hypolepis*-type. Lateral folds and vascular tissue continuous with them, *black*. From Tansley and Lulham.

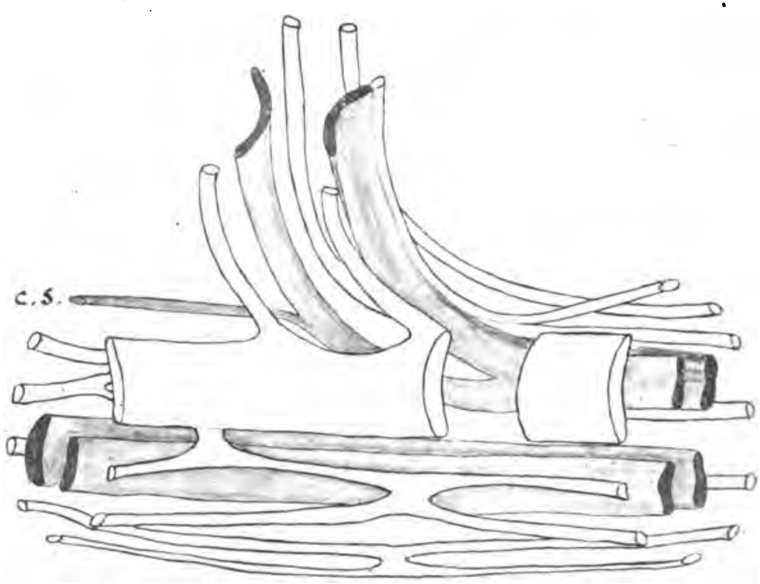

Fig. 67. *Pteris aquilina.* Vascular system of node seen from dorsal side, somewhat simplified. Internal system and lateral folds of leaf-trace darkly shaded. A portion of the dorsal meristele of the outer cylinder is cut away to show branching of internal strands. *c.s.*, compensation strand. Tansley and Lulham.

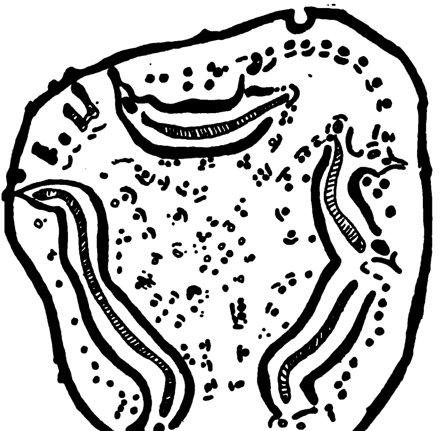

Fig. 68. *Cyathea Imrayana.* Transverse section of stem showing three leaf-gaps, with band-shaped cauline meristeles between. Leaf-traces consist of numerous strands. Small isodiametric accessory vascular strands are seen in the pith and in the cortex. Sclerenchyma, *black.* From De Bary.

of *Pteris*, while by far the most important function of the internal vascular system is to supply the deep lateral folds of the petiolar system, it is quite possible that in *origin* it may be an elaboration of the leaf-gap margin, as in *Matonia*. Evidence from the structure of the young plants is needed to settle this question.

Dictyostelic Cases.

The vascular system of the Cyatheaceæ (Fig. 68), the typical tree-ferns, is a polycyclic dictyostele, though the internal vascular system is of distinctly different type from most of the forms hitherto considered. The main vascular system consists of a very wide dictyostele, the band-shaped meristeles with their sheaths of sclerenchyma, as seen in transverse section, extending from the edge of one leaf-gap to that of the next, near the periphery of the bulky stem. The curved leaf-trace rapidly breaks up in the base of the petiole into a number of separate nearly isodiametric strands, kidney-shaped in cross-section. The outline of the whole system of petiolar strands has practically the same form as in the two species of *Pteris* just described, but the free edges of the curve are bent in abaxially (Fig. 69, A) as in the young *Matonia*. In addition to the primary system of the stem there are a number of isodiametric strands scattered in the pith. In *Cyathea Brunonis* (Fig. 69), one of the simplest types of the genus, four of these internal strands run up into each leaf-gap, two joining onto the two leaf-trace strands situated at the bottom of the deep lateral folds on each side (*a*) while the other two bifurcate, one branch of each (*c*) joining the strands at the adaxial outer corners of the lateral folds, the others (*b*) joining the strands forming the incurved free edges of the trace (Gwynne-Vaughan '03). Here then we have

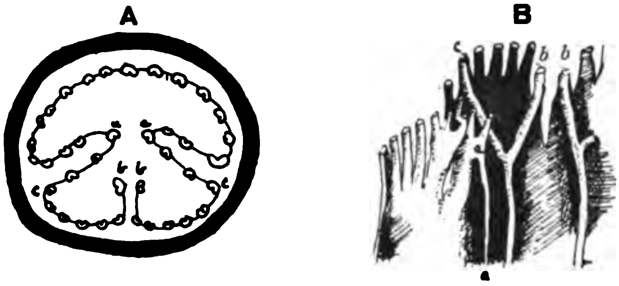

Fig. 69. *Cyathea Brunonis.* A.—Transverse section of base of petiole showing vascular curve with deep lateral folds and incurved ends, consisting of a number of small kidney-shaped meristeles *a*—*a*, *b*—*b*, *c*—*c*, strands to which internal accessory strands of the stem have joined.

B.—Leaf-trace seen from within. *a*, *b*, *c*, internal accessory strands joining certain strands of leaf-trace curve. From Gwynne-Vaughan.

the internal strands of the stem entirely devoted to the petiolar vascular system, partly supplying the lateral elaborations of the trace, as in *Pteris*, and partly supplying the incurved free edges of trace as in *Matonia*. Traced downwards, the internal strands end blindly in the ground-tissue of the pith. Whether they represent a comparatively new accessory system, or whether they are to be regarded as a reduction from a more highly developed internal system in some ancestor of the Cyatheaceæ, in which the external vascular ring was narrower than at present, we have scarcely the data to decide. In other species of *Cyathea* the relations are more complex. In the young plants of *Alsophila excelsa* (Gwynne-Vaughan, '03) the internal strands first appear at about the level of the tenth leaf in the form of internal thickenings of the xylem of the stele just below the point of origin of the two adaxial leaf-trace strands (representing the free edges of the trace-system). In the case of later nodes these thickenings become free during their downward course, and end blindly in the central ground-tissue.

In addition to the medullary vascular strands certain accessory cortical strands exist in some species of *Cyathea* (Fig. 68) and *Alsophila*, but the nature and origin of these is not understood.

Ceratopteris thalictroides is an annual aquatic fern of isolated systematic position with a polycyclic dictyostelic adult stem evidently much reduced, and bearing crowded leaves. The vascular system of the young plant is a simple dictyostele, but the older plant appears to possess a perforated dictyostele, with a number of weak internal accessory strands, some of which end blindly below, and which appear to pass into the base of the petiole and there to fuse with the outer strands derived from the primary cylinder (Ford, '02). Whether the internal cauline strands have any direct connexion with the internal petiolar strands, of which there may apparently be a good many, is not clear from the available accounts, nor is it obvious whether there is or is not a connexion between the internal accessory strands and the outer cylinder of the stem.

Marattiales. This very old group of ferns stands apart, in many respects, from all the rest, and although its members conform to Bower's type of the Simplices, it may well be maintained on anatomical as well as on other grounds, that they are better kept quite apart from the Leptosporangiate families that we have hitherto been considering. From the purely anatomical point of view they exhibit the most complicated structure of any known types, the most highly developed form of polycyclic dictyostely. Thus they come naturally at the end of the series of cases we have been discussing, though it is quite certain that they have no direct phylogenetic connexion with any of the Ferns we have already dealt with. The polycyclic dictyostely of the modern Marattiaceæ is shared by the well-known Carboniferous and Permian tree-ferns, the Psaronieæ, so that we are obliged to believe that the factors giving rise to these highly complex vascular systems came into play at a very early period, long before they had become operative in any of the great Leptosporangiate series, perhaps before the Leptosporangiate type appeared at all. It is all the more interesting to find that these now isolated forms show, in connexion with the appearance of these complex characters, phenomena essentially the same as those we have been considering in the Leptosporangiate Ferns.

The well-known tree-fern stems from the Carboniferous and Permian, which, when they are preserved so as to show anatomical structure, are placed in the genus *Psaronius*, are almost certainly of Marattiaceous affinity. Both the evidence of association with Marattiaceous sporangia, and also many anatomical details, point in this direction. In habit, however, the Psaronieæ were lofty tree-ferns, even taller than the modern Cyatheaceæ, and in the general structure of their vascular systems, they have something in common with this family, though scarcely enough to justify the conclusion of Stenzel, and of their most recent investigator, Rudolph (05), that they have a real affinity with the modern tree-ferns.

Like the living *Angiopteris*, the Psaronieæ are highly polycyclic, from five to seven distinct vascular rings occurring in the stems of some forms; but, unlike those of the Marattiaceæ, the outermost vascular cylinder is not perforated, so that the meristeles are for the most part broad and band-shaped (Fig. 70), indicating, like those of the Cyatheaceæ, a slighter departure from the primitive solenostelic type. In the form of the leaf-trace also, *Psaronius* is relatively primitive, its cross-section being C-shaped with incurved ends, rather like that ot a *Dicksonia*, and indeed the structure of the complicated vascular system of the stem, and its relation to the leaf-traces, show a close resemblance to the solenostelic *Saccoloma* (*Dicksonia Lindeni* Hk).

The species[1] of *Psaronius* are divided by Zeiller ('90) into three groups according to the arrangement of the leaves: the distichous, the tetrastichous (decussate) and the polystichous (spiral). Perhaps the distichous arrangement—unknown in modern tree-ferns—is the primitive leaf-arrangement. From our present point of view a general description of the anatomy of the genus will suffice.

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[1] *i.e.*, distinct types of structure. It may very well be, as Zeiller points out, that in some cases different "species" may represent different stages of development of one form, and on the other hand, more than one species in the ordinary sense may be comprised in a single anatomical "species."

The external vascular ring (Fig. 70) consists of a number of peripheral strands, each U-shaped in cross-section, with the concavity of the U facing inwards, and separated one from another by radial bands of sclerenchyma. Every alternate strand of this peripheral series is a leaf-trace (*l.t.*, Fig. 70), while the intermediate strands (*stèles peripheriques* of Zeiller) are cauline (*c.st.*, Fig. 70). The internal cylinders consist of series of curved band-shaped strands, the edge of each strand being more or less approximated to that of its neighbour. In passing up the stem a series of anastomoses occur between the successive cylinders in a radial line corresponding with a leaf-orthostichy, and this ends by the passing out of a strand from the penultimate cylinder. This strand fills the gap caused by the departure of the leaf-trace immediately below, receives contributions from the "peripheral stele" on each side, and itself becomes the leaf-trace supplying the next leaf of the orthostichy. The exact method of anastomosis between the different strands varies in different types. The gap-filling strand sometimes comes into actual connexion with the adjacent "peripheral steles," and sometimes receives off-shoots from them, but the general method is always the same in those cases in which the details have

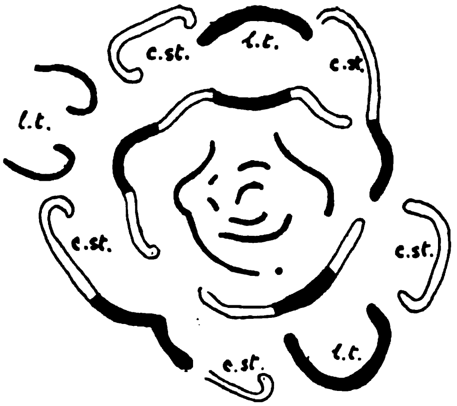

Fig. 70. Diagrammatic transverse section of vascular system of a polystichous *Psaronius*, showing five dictyostelic concentrically arranged cylinders. *c.st.*, cauline meristele; *l.t.*, leaf-trace. From Rudolph after Zeiller.

been followed. It will be seen that the sequence of events is exactly that which obtains in *Saccoloma adiantoides.* A strand from the second cylinder moves out to fill the leaf-gap in the outer one, and the gap so made is filled by a branch from the next, and so on. The main difference is that the strand which fills the gap in the outer ring at once becomes a clearly defined and separate leaf-trace, instead of merely forming part of a continuous cylinder. The agreement extends to the formation of the ends of the leaf-trace curve by strands arising from the sides of the leaf-gap, *i.e.* in *Psaronius* from the adjacent "peripheral steles."

Thus the vascular system of *Psaronius* agrees perfectly with the polycyclic solenostelic types, and though we have, of course, no evidence as to its devolopment, we may conjecture that the internal systems of this type had an origin similar to that which obtains in the *Dennstædtia-Matonia* series. While, as has already been said, it is extremely unlikely that the Psaronieæ have any direct connexion with the Cyatheaceæ or with any polycyclic leptosporangiate form, there is something to be said for the view that the Cyatheaceous type, with its blindly ending medullary strands connected with the leaf-trace, is derived by reduction from a more highly developed polycyclic type, somewhat like *Psaronius*, but in which the internal strands, or some of them, had been drawn into contributing to the leaf-trace.

Marattiaceæ. Five genera belonging to this family are known to exist at present and of these we now have a fairly complete knowledge. The leaves in all cases are relatively large, with big leaf-bases. The young plants of all the genera, so far as they are known, have elongated stems. In *Kaulfussia* the adult plant has a creeping dorsiventral rhizome bearing a single row of leaves on its upper surface. *Danæa* has an elongated, but vertical or obliquely directed, rhizome with radial structure. In *Archangiopteris* the rhizome is radially organised and comparatively slender, while in *Marattia* and *Angiopteris* the adult plant has a short thick rhizome, with huge leaf-bases covering almost the whole of its surface.

So far as the adult plants are concerned the simplest type of vascular structure is found in *Archangiopteris* (Gwynne-Vaughan '05). The vascular system of the stem is dictyostelic (Fig. 71), consisting of two to four small strands which anastomose irregularly, and usually a small internal accessory strand (*i.s.*) in addition. The internal strand is free for the greater part of its length, but approaches the cylinder and fuses with those meristeles which are about to close the leaf-gap. Then it separates again and passes slowly across the central ground-tissue to the next leaf-trace above. Gwynne-Vaughan found the internal strand, traced downwards, ending blindly in the pith in one place, so that just below that point the dictyostelic cylinder alone was present (Fig. 71, A). The roots

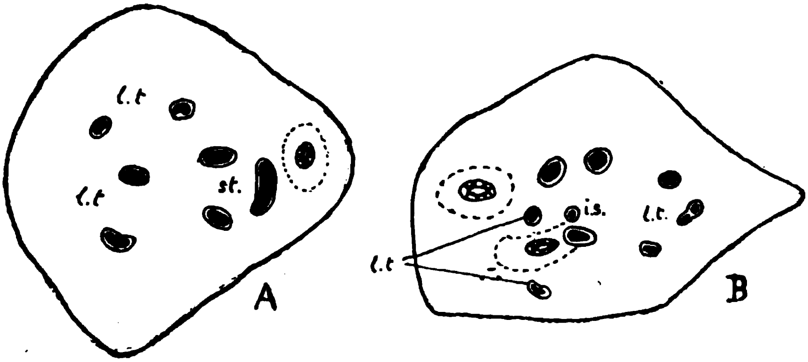

Fig. 71. *Archangiopteris Henryi.* Transverse sections of stem. *st.*, stele ; *l.t.*, leaf-trace ; *i.s.*, internal accessory strand. From Gwynne-Vaughan.

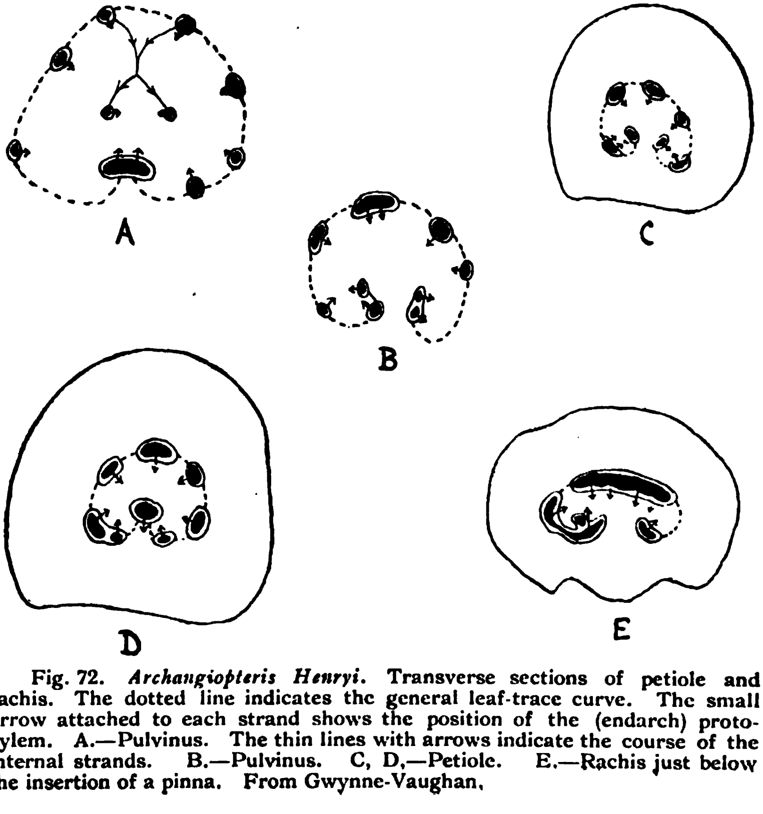

Fig. 72. *Archangiopteris Henryi.* Transverse sections of petiole and rachis. The dotted line indicates the general leaf-trace curve. The small arrow attached to each strand shows the position of the (endarch) protoxylem. A.—Pulvinus. The thin lines with arrows indicate the course of the internal strands. B.—Pulvinus. C, D,—Petiole. E.—Rachis just below the insertion of a pinna. From Gwynne-Vaughan,

arise from the external and lateral faces of the cauline meristeles, one invariably from the point where the internal strand fuses with a meristele of the ring, so that a direct water channel exists between this root and the next leaf above.

Two strands only are given off to supply the petiole. As they pass outwards they divide into several (eight or nine) separate strands, which are arranged, in the base of the petiole, in a typical horseshoe-shaped curve (Fig. 72). The terminal strands of the curve advance towards the median (vertical) plane of the petiole, and at one point in the pulvinus they fuse to form a single broad strand, the protoxylems of which face abaxially (Fig. 72, A). Higher up they become separate again, and curving gradually inwards, they rotate at the same time, so that their protoxylems (endarch) come to face towards the sides of the petiole (B and C). Internal accessory strands, quite distinct from those of the primary curve, and having no connexion with the internal strands of the stem-cylinder, occur in the pulvinus at the base of the petiole. Two of these arise as internal branches of the abaxial strands of the primary curve, fuse together, separate again (A), and travel slowly across the internal ground tissue, to fuse with the two terminal strands of the primary curve (B). These internal strands, not belonging to the primary vascular curve of the petiole, are found in all the genera of Marattiaceæ, and are one of the characters separating this group from other Ferns.

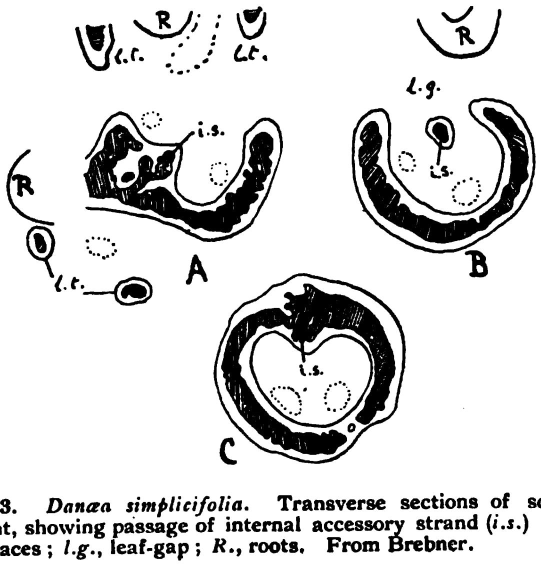

Fig. 73. *Danæa simplicifolia.* Transverse sections of solenostele of young plant, showing passage of internal accessory strand (*i.s.*) across pith; *l.t.*, leaf-traces; *l.g.*, leaf-gap; *R.*, roots. From Brebner.

The vascular supply of the pinnæ is worthy of note. Each pinna receives two strands from the rachis. One of these is large and comes from the side of the curve. The other is small and comes from the incurved end of the terminal strand on the same side, travelling outwards along the inner side of the curve (Fig. 72, E) to pass out to the pinna. Similar phenomena have been found in the other genera of Marattiaceæ. The effect of this arrangement is to supply each pinna with water partly through a channel derived from the terminal strand, which has itself received a branch derived from the strands of the main abaxial curve. This arrangement is to some extent parallel with that of the internal strands of the stem, the supply of the pinna bearing somewhat the same relation to the

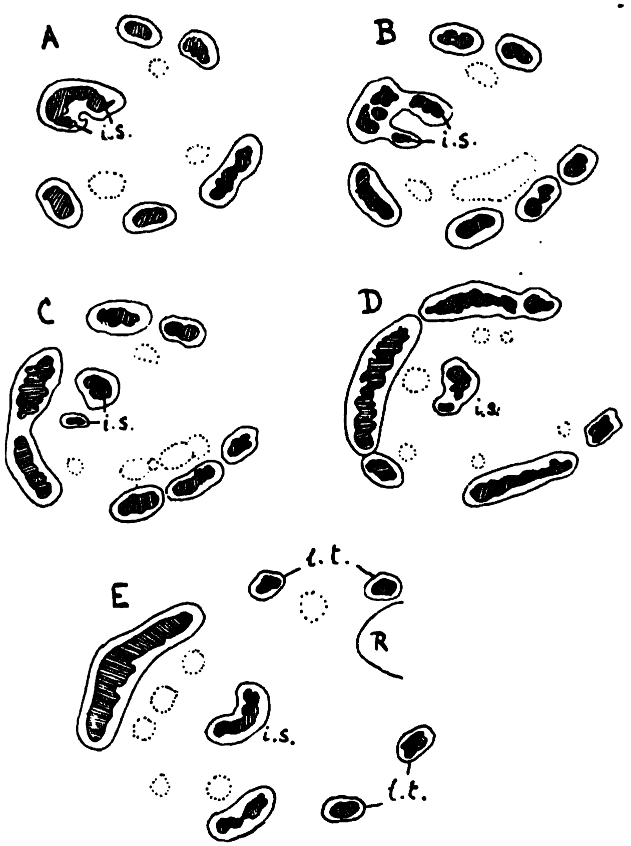

Fig. 74. *Danæa simplicifolia.* Series of transverse sections of vascular system of older stem, with perforated dictyostelic structure, illustrating passage of internal strands into pith, where they fuse into one. Letters as in Fig. 73. From Brebner.

petiolar system, as the supply of the whole frond does to the stem system.

In the stem of the young plant of *Danæa simplicifolia* we at first have a solenostele, (Fig. 73) afterwards a perforated dictyostele (Fig. 74), but the behaviour of the internal strands is fundamentally like what we have seen in *Archangiopteris*, except that the internal strand sometimes branches into two in its course across the central ground tissue (Fig. 74), the branches afterwards again fusing into one (E).

Brebner ('02) points out that the internal strands serve to connect directly the root-insertions (at the points of closure of the leaf-gaps) with one another, and that from the large curved strands formed at these points the leaf traces are given off. Any given root probably does not reach the soil till after the related leaf has unfolded; hence the advantage of a direct channel from roots already developed below to supply the unfolding leaf.

The adult structure of the *Danæa* stem (Fig. 75) appears to

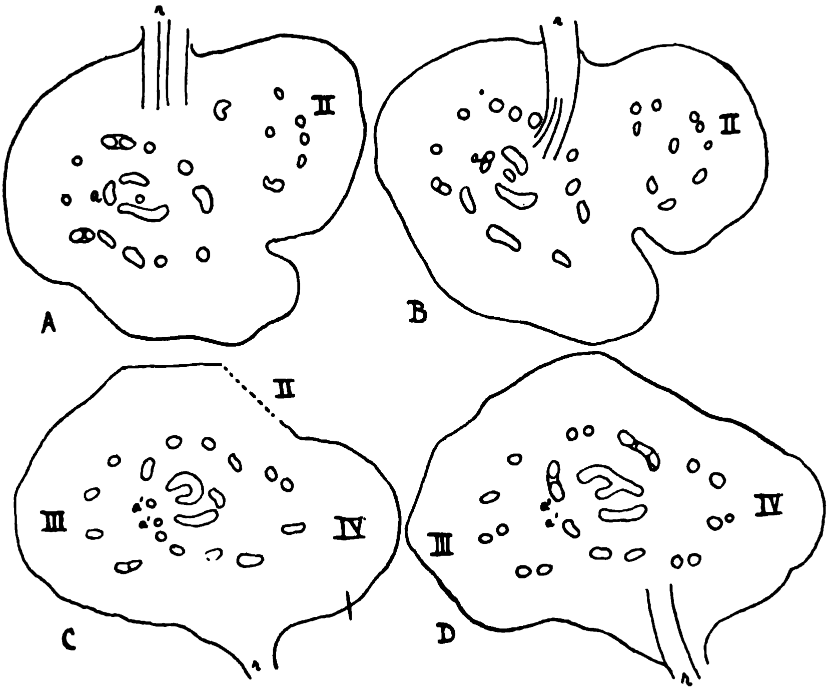

Fig. 75. *Danæa* sp. Series of transverse sections of stem, showing a perforated dicyclic dictyostele, just passing to the tricyclic condition. II., III., IV., successive leaf-bases. In A and B leaf-trace II. possess an internal strand. a, a' compensation strands from second cylinder filling gap III. in the outer one. *r.*, roots. From Rudolph.

differ from the young condition only by the presence of a greater number of leaf-trace strands, which branch and anastomose freely. The petiolar structure corresponds in a general way with that of *Archangiopteris*, though the petiole possesses more internal strands.

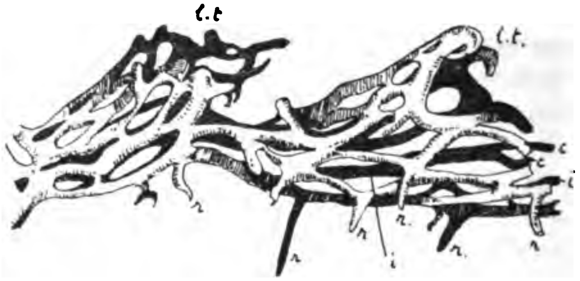

Fig. 76. *Kaulfussia æsculifolia*. Vascular skeleton including two nodes. *l.t.*, leaf-traces; *i.*, internal strand, which sends off a dorsal branch below each leaf-insertion. This dorsal branch splits into two (*c.*, *c.*) which eventually help to close the leaf-gap. *r.*, roots. From Kühn.

Kaulfussia differs from the types already described in having a creeping rhizome with definitely dorsiventral structure, bearing roots on its sides and lower surface, and two rows of leaves on the upper side. The vascular system (Fig. 76) consists of a much perforated solenostele[1] but in this case only the dorsal portion is concerned in the bearing of leaf-traces, and its meshes are much

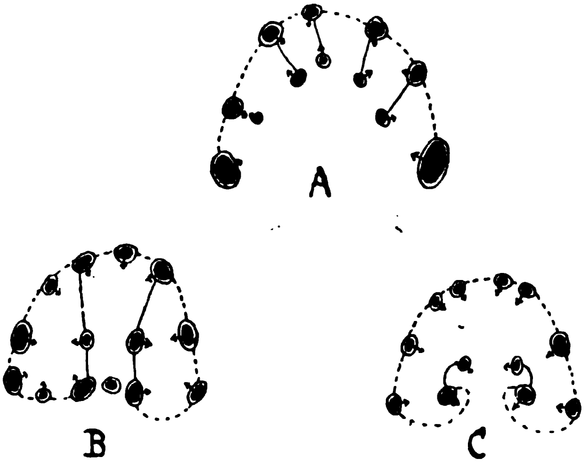

Fig. 77. *Kaulfussia æsculifolia*. A.—Vascular strands of base of petiole. B.—Lower part of petiole. C.—Upper part of petiole. See explanation of Fig. 72. From Gwynne-Vaughan.

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[1] If we define a dictyostele as possessing overlapping *leaf*-gaps.

shorter than the ventral ones. Several strands pass off to the petiolar system, leaving a well-marked leaf-gap. There is an internal strand (*i.s.*) which runs freely in the central ground tissue towards the lower side, and sends up a branch, which divides into two, or two separate branches, below each leaf-gap. These join on to the strands bounding the gap and close it in front. Here then the behaviour of the internal strand may be compared with that of the internal cylinder of *Matonia*, while *Danæa* may be compared with *Saccoloma*.

The basal pulvinus of the *Kaulfussia* petiole (Fig. 77) shows the same phenomenon that we saw in *Archangiopteris*, but the internal strands which leave the abaxial strands of the arc and cross to the adaxial terminal strands are more numerous than in that genus. The internal strands are not continued up as such above the pulvinus, but the two terminal strands, with which they have joined, fuse together in the median plane, and sink into the centre of the petiole as a large strand with adaxially directed protoxylems. This large internal strand is continued up into the rachis of the frond and contributes branches to the pinna-traces.

In *Marattia* and *Angiopteris* the stem of the adult plant is not elongated, but thick and fleshy, with the surface completely covered by the huge leaf-bases. The young plants however show the elongated form and their organisation is essentially radial, the leaves being given off all round, though in the adult plants there is a distinct tendency to dorsiventrality. In the young plants the vascular system is organised in fundamentally the same manner as in the genera already described, a ring of branching and anastomosing strands surrounding a central one, which behaves as in the other cases.

In the adult stem of *Marattia fraxinea*—a comparatively small species—there are two concentric rings of strands, *i.e.*, two dictyostelic cylinders surrounding a central strand. The second cylinder here closes the leaf-gap, as the central strand does in the simpler forms, and is nearly equivalent to the second solenostelic cylinder in *Matonia pectinata*. There is little doubt that, as in that case, it arises ontogenetically by elaboration of the original internal strand, though there is no available information on the point. The internal strand of the adult stem fills the gap made in the second cylinder by sending up two branches to the point of closure, again just as in *Matonia*, and the whole arrangement is materially the same.

The petiole of *Marattia fraxinea*, at the level of the pulvinus, shows either a single circle of strands enclosing a central one, or two concentric circles enclosing a central strand, as in the stem.

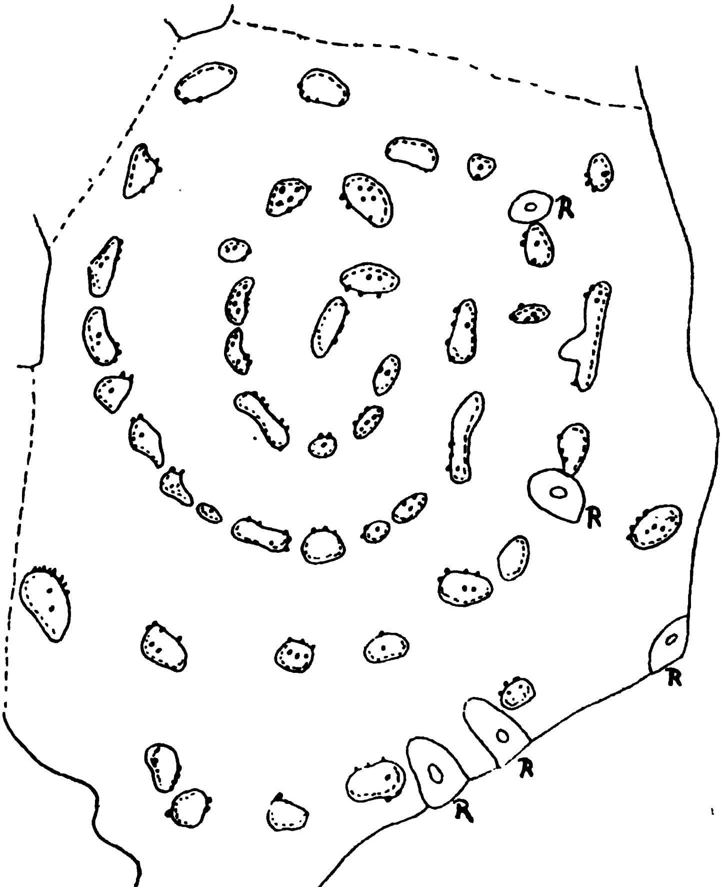

Fig. 78. *Angiopteris evecta.* Transverse section of stem showing four or five concentric circles of meristeles. The circles tend to run one into the other, giving a spiral arrangement. Protophloems represented by dotted lines; protoxylems by larger dots. The dotted lines bounding parts of the section represent leaf-bases cut away. *R*, roots. From Shove.

None of these internal strands is directly connected with any cauline strands, but they arise by branching of members of the outer circle, *i.e.* of strands belonging to the original leaf-trace curve. Traced upwards they disappear by successive fusions, first of the central strand with an adaxial member of the internal ring, then of the strands of this ring with the adaxial members of the outermost ring. This takes place so gradually that a number of the internal strands continue their course above the pulvinus right up into the region of the rachis.

Angiopteris evecta, as is well known, exhibits, in its huge fleshy stem and leaf-bases, the most complicated type of vascular system known, not only in Marattiaceæ, but in any Fern, living or extinct. Nevertheless it is quite clearly an elaboration of the simpler Marattiaceous type along the lines we have already traced. In place of the two or three concentric dictyostelic cylinders of *Marattia*, large stems of *Angiopteris* may show as many as nine distinct concentric circles of strands as seen in transverse section (Fig, 78).

The adult stem, comparatively narrow at the base, rapidly increases in size towards the apex. In the specimen examined by Miss Shove ('01) the stem had a length of 25 cm., and was 8 cm. broad at the top, tapering to 1 cm. at the base. The dorsiventral structure of the base was well-marked, the lower surface being destitute of leaves but thickly covered with roots for a distance of 8 cm. from the basal extremity. At the apex the stem was nearly radial in structure, correlated with the diminished production of roots. The meshes of the vascular network are much larger on the ventral root-bearing, than on the dorsal leaf-bearing side. "The roots originate, a few in the outer, the majority in the inner zones" of vascular strands, some actually arising from the strands situated near the upper surface of the stem, penetrating most of its thickness and emerging on the lower surface. At the base of the stem the vascular system is simple, increasing in complexity upwards, in exactly in the manner described in the other genera, till a number of concentric, highly dissected dictyostelic cylinders are formed. Owing to the shape of the stem each of these "cylinders" has the general form of an inverted cone, as pointed out by Mettenius ('65). As each leaf-trace, consisting of several strands of the outermost cylinder, passes off, a segment of the second cylinder moves out to fill the gap, its strands anastomosing right and left with those of the outer cylinder bordering the leaf-gap (Fig. 79). Owing to the crowding of the leaf-insertions, however, a given set of strands remains in the outer cylinder for a very short distance only, the compensating strands which have filled any given gap almost immediately contributing to the traces of higher leaves. Segments from the third cylinder fill up the gaps in the second in the same way, and so with the successive inner cylinders.

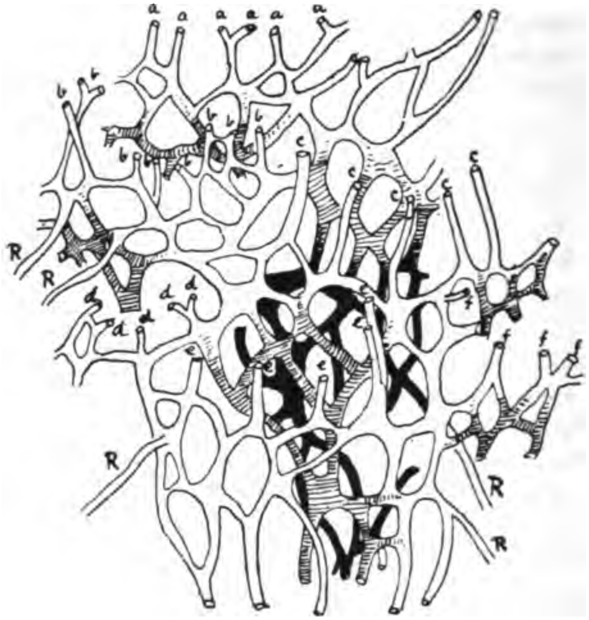

Fig. 79. *Angiopteris evecta.* Part of vascular skeleton of dorsal side of stem seen from without, to show the rapid passing out of strands from inner cylinders to fill the gaps made in the outer one by the departure of the leaf-traces. *a*, *b*, *c*, *d*, *e*, *f*, designate the strands belonging to different traces. *R*, root-steles. The outer cylinder is left white; the parts of the second cylinder shown are shaded; the third cylinder, only represented in a small part of the figure, is black. After Shove.

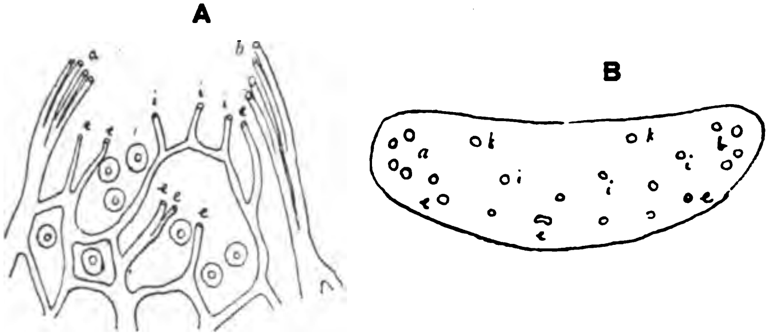

Fig. 80. *Angiopteris evecta.* A.—Vascular skeleton of leaf-base. B.—Transverse section of base of petiole. *a*, *b*, lateral groups of strands of the leaf-trace. *e*—*e*, external strands forming the abaxial arc of the trace. *i*—*i*, internal strands arising from *e*—*e* and multiplying by branching. *k* - *k*, strands derived directly from the second cylinder. From Mettenius.

The leaf-trace (Fig. 80) is formed of an abaxial arc of from four to six strands (*e*) and of adaxial wings, sometimes, according to Mettinius, formed from two strong lateral strands, each of which immediately splits into several (*a*, *b*). The same investigator found that two strands (*k*, *k*,) from the second cylinder occasionally contribute to the leaf-trace, either directly, or by anastomosis with strands of the outer cylinder. These second-cylinder strands appear to occupy a position as the terminal strands of the adaxial wings of the leaf-trace (cf. *Matonia*). It should be mentioned that Miss Shove failed to find these strands in the specimen she examined. The number of the leaf-trace strands rapidly increases by branching, and internal strands (*i*, *i*,) arise from those of the abaxial arc as in the other genera.

Thus in the Marattiaceæ we find the internal vascular strands of the stem playing exactly the same part as in the Leptosporangiate Ferns. In the simplest forms there is one internal strand only, which runs from leaf-gap to leaf-gap as in the simplest polycyclic Leptosporangiate types such as *Dennstaedtia adiantoides*. In the more complicated cases the internal system increases in complexity in relation to the increase in size and crowding of the leaves, till the highest grade of complexity is reached in *Angiopteris*. The gap-filling segments of the second cylinder are sometimes drawn into contributing to the margins of the leaf-trace, as in *Matonia*, but typically they do nothing more than fill the gaps in the outer cylinder caused by the departure of the leaf-traces.

On a review of the phenomena of polycycly, which we have been surveying, it is apparent that the primary stimulus to the development of an internal vascular system is the need for providing additional conducting or water-storing tissue at the leaf-gap, when the departure of the trace largely diminishes the conducting capacity of the stele above that point. In some cases the accessory system is drawn into supplying the leaf-trace directly, owing apparently to the ease with which parts of a petiolar system undergoing progressive complication may become attached to the internal system at its point of junction with the edge of the gap. In other cases (*Pteris*) the main function of the internal system is to supply directly the complications of the leaf-trace, of which it then appears to be a decurrent development, but in such cases the internal system always seems to help fill the leaf-gap, though it may be in a very small degree, and the possibility is not excluded that that was its original function even here. More evidence is however required on this point.

In the simpler polycyclic forms of solenostely, the internal strands are not directly connected with roots, and must be regarded simply as water reservoirs, filled and emptied through the nodal connexion. The internal system reaches its highest degree of efficiency only in dissected types like *Angiopteris*, in which the internal systems have a direct supply of their own from independent roots.

ON THE SORUS OF *DIPTERIS*,

By Helen M. Armour, M.A., B.Sc.,

Robert Donaldson Scholar, Glasgow University.

[Figs. 11—14.]

FROM time to time since 1823 the external characters of the genus *Dipteris* have been described, and its division into four species has been established. Its systematic position has also been discussed by various authors, such as Brown, the earliest of these, Moore and Hooker, and later by Christ and Diels. But the latest and most detailed description of the family is contained in the account published by Mr. Seward and Miss Dale in 1901 of "The Structure and Affinities of *Dipteris*, with Notes on the Geological History of the Dipteridineæ." This paper is based mainly on a study of *Dipteris conjugata*, of which material was obtained both from Borneo and the Malay Peninsula. Most attention is devoted to the anatomical structure of this one species of the family, but the detailed account is prefaced by a general survey of the whole group, which embodies the results of the earlier workers. The appearance of each species is noted, and then it is stated that "the sori which are without an indusium, consist of numerous sporangia and filamentous paraphyses terminating in glandular cells: the sporangia are characterised by the more or less oblique annulus and by the small output of bilateral spores; the sporangia of the same sorus do not develop simultaneously."[1]

Detailed investigation of one of the other species, *Dipteris bifurcata* (*Lobbiana*), has shown various points of difference which have seemed worth recording.

The material used for this study was brought from the slopes of Mount Ophir, in the Malay Peninsula, by Dr. W. H. Lang, of Glasgow University. Since it included favourable specimens of the younger stages as well as those more mature, it was possible to trace satisfactorily the development of the sporangium in addition to the structure of the sorus.

In *Dipteris bifurcata* the sori are situated on the under surface of the narrow lamina in two regular rows, one on either side of the midrib (Fig. 12.) Each sorus is immediately above a small vascular bundle and practically fills up the centre of the areola formed by the lateral veins given off by the midrib. The earliest stage shows the receptacle as a flat area of small celled tissue, which by division has formed two layers. The cells are differentiated from those of the epidermis by their small size and deeply staining contents. Usually the area is longer than its breadth, and the number of cells in its length varies from 15 to 25, or even more in some cases. The first indication of the sorus is the upgrowth of most of these small cells to form papillæ, which are the rudiments of the paraphyses (Fig. 11, 1). Divisions take place in these once or twice before any trace of sporangial development appears. Then the superficial cells of the receptacle which have not grown out as paraphyses enlarge and their nuclei become denser and more granular. Each projects as a dome-shaped cell, which soon shows sporangial segmentation resembling that found in the group of the "Gradatæ" (Fig. 11, 1—3). A later stage shows each sporangium surrounded by a circle of paraphyses, whose enlarged end-cells arch over, forming a sheath-like structure to enclose the sporangium (Fig. 11, 3). Later stages still, however, show the paraphyses quite outstripped by the sporangia, which grow rapidly and completely cover the receptacle (Fig. 11, 4). The paraphyses do not extend beyond the lowest cells of the annulus of the mature sporangium.

Fig. 11, 4 shows a fully-developed sorus, which contains, on an average, 35 sporangia closely packed together. There is no definite grouping of the sporangia with reference to a central point.

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[1] Seward and Dale. Phil. Trans. B., Vol. 194, p. 492.

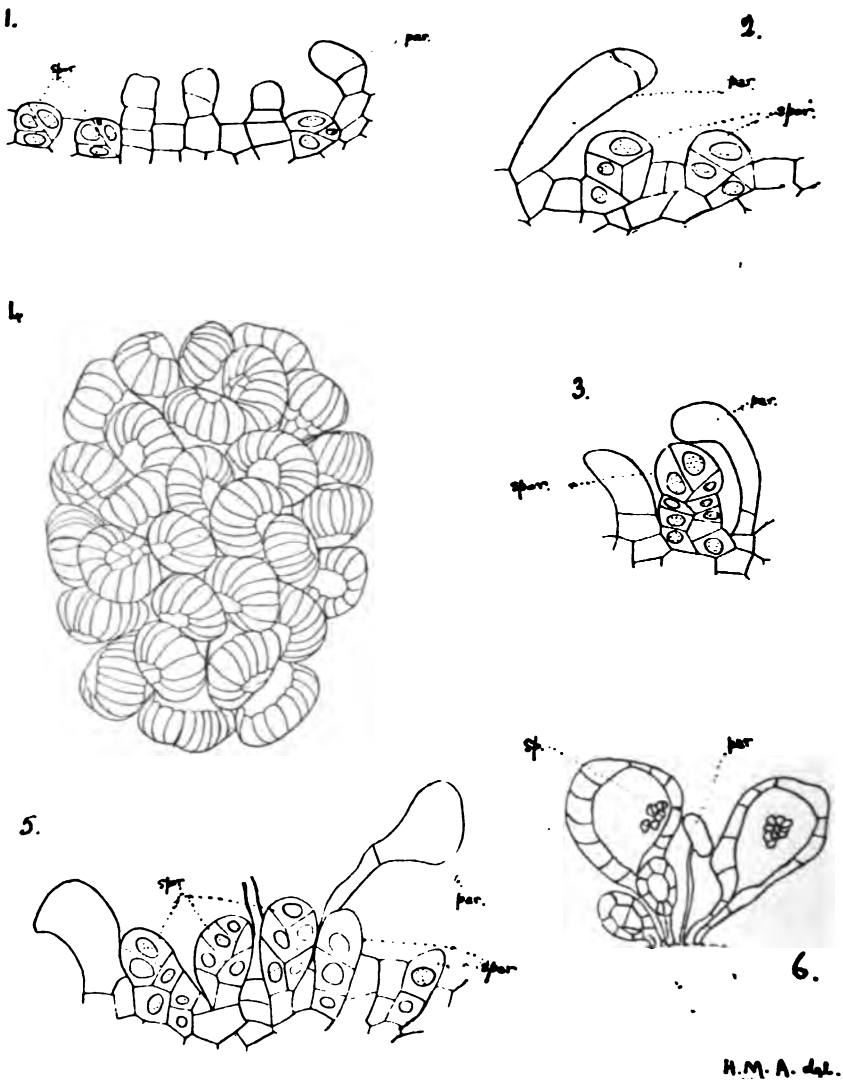

Fig. 11.

1. Transverse section of part of very young sorus of *Dipteris bifurcata* showing paraphyses and young sporangia. *spor.*, sporangium; *par.*, paraphysis. × 340.

2. Transverse section of older sorus of *Dipteris bifurcata*. *spor.*, sporangium; *par.*, paraphysis. × 340.

3. Median longitudinal section of sporangium of *Dipteris bifurcata*. *spor.*, sporangium; *par.*, paraphysis. × 340.

4. Surface view of whole mature sorus of *Dipteris bifurcata*. × 55.

5. Transverse section of sorus of *Dipteris conjugata* showing sporangia of various ages. *spor.*, sporangium; *par.*, paraphysis. × 340.

6. Transverse section of older sorus of *Dipteris conjugata* showing "Mixtæ" condition. *sp.*, spores; *par.*, paraphysis. × 110.

On the contrary, the method of arrangement and the character of the sporangia would seem to indicate that every available part of the flat receptacle had been utilised to provide for the production of spores. The paraphyses in section appear as short club-shaped structures with the end cell colourless and elongated. In *Dipteris bifurcata* the sporangium is large. It has a broad complete annulus, which appears curved or twisted owing to the unequal development of the two faces of the sporangium, for the concave face is narrow, consisting of merely two rolls of elongated cells, while the convex face is broad and bulged out, showing four or five rows of larger cells. The narrow face is the one exposed. There is a definite stomial region which is situated to the right or left side of the narrow face according to the position of the sporangium in the sorus.

Throughout all the stages of the sorus in *Dipteris bifurcata* it is plain that the sporangia contained in it are all of the same age, *i.e.* they develop simultaneously.

The distribution of the sori on part of the under surface of the large frond of *Dipteris conjugata* is shown in Fig. 13. In accordance with the description already given by other writers, it will be seen that the sori "vary in size and shape," and are "often confluent." Compared with the mature sorus of *Dipteris bifurcata*, the sorus of *Dipteris conjugata* is small, and may contain from twelve to seventeen sporangia, loosely arranged and separated from one another by the paraphyses, which have the terminal glandular cell much bulged and of a rich brown colour. The sporangium also is small, but shows the main characters of the sporangium of the other species. As has been noted, the annulus is oblique. The ripe sporangia in the specimens examined gave clear evidence of the presence of a definite stomium. The material of *Dipteris conjugata* from Mount Ophir did not afford any specimens showing the youngest stages of the sorus. The earliest stage observed is shown in Fig. 11, (5) which illustrates the fact, already stated by Seward and Dale, that the sporangia in this species do not arise simultaneously. This is still more clearly shown in (6) representing a more mature state.

The genus *Dipteris* thus includes one species, *Dipteris bifurcata*, which shows simultaneous development of the sporangia in each sorus and conforms, therefore, to the "Simplices" in Professor Bower's classification, and another species, *Dipteris conjugata*, having sporangia of various ages present in the same sorus and it conforms, therefore, to the "Mixtæ." The external characters of the frond also give evidence of the difference between them. For *Dipteris bifurcata* has a narrow lamina andlarge sori arranged in regular rows, one on either side of the mid-rib, as shown in Fig. 12, while in *Dipteris conjugata* the lamina is broad, the sori are small and very numerous (Fig. 13). Intermediate between these two species in outline of leaf and distribution of sori comes the species, *Dipteris quinquefurcata* (Baker), Christ, in which the segments are still linear, though broader than in *Dipteris bifurcata*, with clearly marked meshes of the venation in which several sori are situated, in place of the one

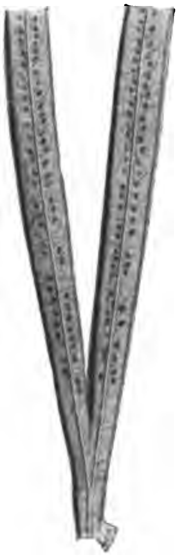

Fig. 12.

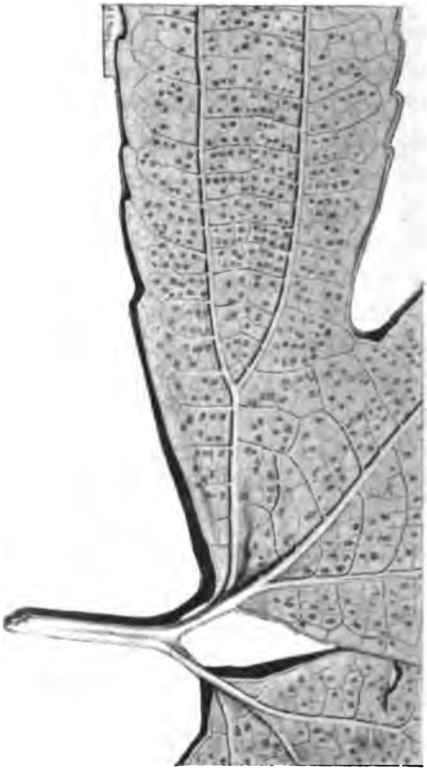

Fig. 13.

Fig. 12. *Dipteris bifurcata* Baker (=*Lobliana* (Hk) Moore) parts of two pinnæ showing narrow form, venation, and regular sequence ot sori. Natural size.

Fig. 13. *Dipteris conjugata*. Rein. Portion of leaf showing extended surface, webbing between the pinnæ, the venation, and numerous sori spread over the enlarged surface. Natural size.

or sometimes two present in the latter species. Fig. 14 was drawn from a specimen, labelled "China Station," from the collection of Captain Hope, R.N. This is probably an example of *Dipteris quinquefurcata*. In any case it shows characters of outline and sori intermediate between *Dipteris bifurcata* and *Dipteris conjugata*. An examination of its sori showed that all the sporangia of a sorus were apparently of the same age, but material was not available for developmental observations.

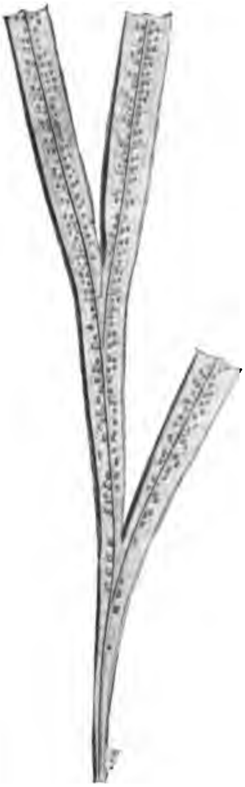

Fig. 14. *Dipteris quinquefurcata* Baker (?) pinnæ showing greater width upwards; below, the sori are in two lateral series, but spread out upwards with many fissions.

From the facts thus obtained it appears that the three species form a series, of which *Dipteris bifurcata* is the most primitive. This species shows the distribution of sori typical of *Matonia*. There appears to have been first a widening of the pinnules in

Dipteris quinquefurcata, and then in *Dipteris conjugata* a webbing of them to form a broad expanse. Parallel with this goes evidence of fission of the sori leading to great increase in their number, together with the reduction in the number of sporangia in each sorus. And finally there is the further progression from a sorus of the type of the "Simplices," with all the sporangia simultaneous, to a condition indicative of the "Mixtæ," where the sporangia of a sorus are of different ages. It must be noted also that such a transition within the genus from a simultaneous to a successive type of sorus is paralleled in the case of the genus *Dennstaedtia*, where, however, the step is from a sorus of the type "Gradatæ" to that of "Mixtæ."[1]

Since the changes in all these characters run parallel, it seems highly probable that they indicate a progression from a type comparable with that of *Matonia* to the broadly expanded type of *Dipteris conjugata.*

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[1] Bower, F. O. ('99). "Studies in the Morphology of Spore-producing Members. Part IV. The Leptosporangiate Ferns." Phil. Trans. B. Vol. 192, Pl. 7, Fig. 132.

THE BOUCHE D'ERQUY IN 1907.

[Figs. 15, 16.]

THE studies on the halophytic vegetation of the Brittany salt-marsh—commenced in 1904—have been continued during the present year. Since the writing of the last report[1] three minor visits have been paid in addition to the annual expedition (lasting from the 1st to the 14th of September) in which twenty persons took part.

Chromatic Instability : Transplantations.

It may be recalled that the more stable portion of the vegetation-covering on the Erquy marsh falls into a limited number of distinct types or associations, *viz* :— the Juncus-zone on the periphery; the Suæda-plateaus, slopes and hillocks, where the annual *Suæda maritima* is thickly scattered through the Glyceria-turf; the Salicornia-flats, crimson in colour, bearing a dense and uniform covering of *S. herbacea*; finally the shallow channels and depressions that occur most characteristically among the Suæda-hillocks and which are remarkable as being the principal habitat of the distinct apple-green form of *S. herbacea.*

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[1] New Phytologist, Vol. V., p. 189.

These associations, being largely composed of plants renewed each year by seed, afford excellent subject-matter for the study of the influence of climatic and other physical factors upon plant-populations. In the general features of their distribution, though subject to minor oscillations, these associations shew a remarkable persistency. But when the annual Salicornia- and Suæda-constituents of the associations are analysed in detail, and the results of successive years compared, indication of extreme instability is manifest. The most striking instance of this instability is afforded, perhaps, by the "apple-green" Salicornia-depressions and channels. In 1904 and 1905 they fully merited the name of apple-green and stood out prominently from the purple and crimson vegetation round about. In 1906 a large infusion of crimson and dingy coloured Salicornias was mingled with the green, so that the channels had lost their distinctive character. The dingy specimens included several shades which tended to connect the reds with the greens. In the present year the channels shew a combination of the features of 1905 and 1906. As in 1906, both red and green Salicornias are present, but they shew an extreme purity of colour (recalling 1904 and 1905) and the dingy intermediate forms were much more rare.

On the Suæda-slopes a somewhat analogous change was noted. The zonation of former years into purple and green Suædas has largely disappeared and a colour mosaic has taken its place. Moreover the Salicornias, which always accompany the Suædas in this association, and which in the past largely consisted of dingy individuals, shew this year a striking infusion of apple-green forms.

Thus each year brings its surprises, and it is impossible to say what fresh chromatic combination may be next revealed. This much at any rate is certain, that we are only just beginning to appreciate the full complexity of the phenomena, the causes of which we would elucidate.

In the report for 1906 some mention was made of an extensive series of reciprocal transplantations carried out to ascertain whether the differently coloured forms breed true from seed, Confining ourselves to a single pair of characters, redness and greenness in Salicornia, a brief account of the results reached is not without interest. The transplantations in this case consisted of interchanging small sods of red and green forms, respectively, at or after the time of flowering. Thus a red matrix was inoculated with green plants and a green matrix with red, in the hope that the inoculations would ripen and shed their seed in the new habitat. This year the systematic examination of the transplantations shewed negative results in a large number of cases, *i.e.* cases in which no traces of the inoculated form were discoverable either on or round about the inoculated sods. But this does not detract from the significance of a considerable number in which the inoculated form had perpetuated itself by seed in the new habitat. The most striking of these "successes" was a series of "apple-green" inoculations in the purest type of "crimson plain" which the Erquy marsh presents. In a majority of these the inoculated sod bore a number (ten or fifteen in some cases) of unmistakable apple-green plants, whilst occasionally the matrix immediately around the inoculation bore similar specimens. As apple-greens are extremely scarce in this crimson plain it is difficult to resist the conclusion that the plants in and about the inoculations must have originated from the parent forms of the inoculation.

That the soil is not the talisman that determines colour follows from several parallel series of transplantations in which the Salicornias were removed and the *soils* alone inoculated. In practically all cases these "transplanted denuded soils" produced the same crop as the adjacent matrix.

Another series of transplantations of *seedlings* still remains to be carried out with a view to studying the influence of changed environment, for of several hundred experiments made in April 1906, the great majority failed altogether owing to the drought that prevailed; whilst, of those that succeeded, most approximated to dingy--but that season, as we have seen, tended to produce dingy everywhere, so that no conclusions can be drawn.

The main result of the transplantation experiments would seem to be the establishment of the fact that colour, in the case of apple-green, breeds true and propagates its like in an environment which normally produces only reds. The same result is indicated in at least one other case, but the evidence is less abundant.

The transplantations are of course intended merely to serve as the precursor of more critical breeding experiments—which would have been in full progress but for unforeseen mishaps. The annual halophytes should prove admirable material for such a purpose in view of the abundance of seed produced and its ready power of germination. Moreover, Salicornia does not appear to offer any insuperable obstacle to hybridising experiments. On the other hand, the conditions best calculated to bring out the differentiating colour-characters are not altogether easy to secure away from the salt-marsh. Some of these practical difficulties are on the way to solution; meanwhile it is proposed to carry out experimental cultures in a portion of a reclaimed meadow where, owing to percolation, halophilous conditions still prevail. Experiments of this kind on the marsh itself are precluded owing to liability of contamination by foreign seed brought by the tide.

CROSS-POLLINATION.

Before leaving this part of the subject it may be mentioned that experiments commenced in 1906 and continued this year shew that a fairly wide dispersal of pollen-grains by the agency of wind is a normal occurrence on the marsh. The amount of pollen thus carried on a breezy day, taken in relation to the duration and distribution in time of the flowering periods of the various forms (e.g. *S. herbacea*, red and green forms; *S. radicans*) would account for a good deal of crossing, should the existence of hybrids be suspected on other grounds. Indeed, considering all the circumstances, so far as they are known, the conditions for the natural production of hybrids on the Erquy marsh could hardly be more favourable.

MARSH-BUILDING.

Another branch of work to which a good deal of attention was devoted this year was the process of marsh-development.

Broadly speaking a salt-marsh represents one of the ways in which the waste products of the land are worked up once more into vegetation-bearing ground. The character of the Brittany coast favours the erosion of the rock, and the resulting particles finding their way on to the beach are blown above tide-level to form sand-dunes or they are carried up the "Bouche" by tidal currents. Moreover, the dune-spit which closes in the estuary has had a good deal of sand cut away during the last few years, so that there is an abundance of supplies of the raw materials for marsh-building available. That these conditions coincide with a phase of active growth in the marsh itself is not surprising. The general map of the area constructed in 1904, when compared with the present condition of the marsh, shews that active change is in progress in many places (cf. Fig. 15, A, A¹ and B), whilst considerable tracts of bare sand are now in various stages of early colonisation by halophytes. Reference to old photographs dating back to the same period serves only to confirm the evidence of the map, whilst

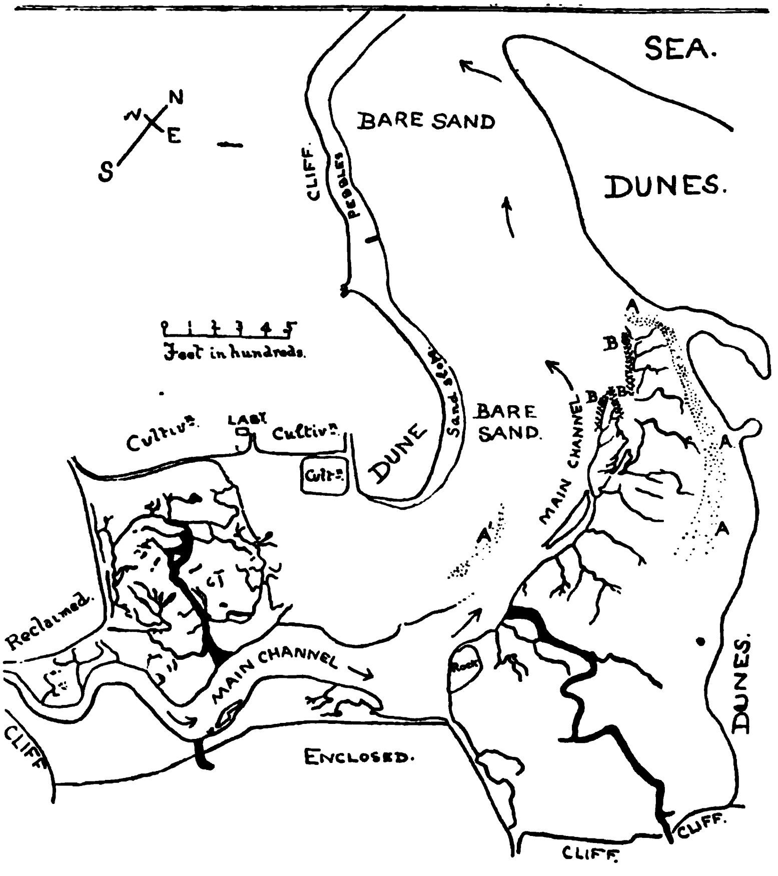

Fig. 15. Sketch map of the Bouche d' Erquy shewing the complex system of natural irrigation-channels by which the tide gains access to the marsh. The plant-associations are not represented. The areas adjacent to the two principal channels (heavy black) consist of established turf, whilst the region on the right, running up to the dunes, corresponds to an earlier phase of development. The shading at A—A and A¹ marks the pioneer zones of *Salicornia radicans*, whilst at B—B (cross-hatching) *Salicornia ramosissima* plays an analogous rôle. The banks of the main channel are not drawn in its lower part, but its course is indicated by arrows. Scale 1/8750.

not a few of the typical "stations" that have been charted from year to year shew a change of type pointing to a definite succession or development in the vegetation-covering.

Nowhere on the marsh has the advance been more striking than in its lower part, where the vegetation abuts on the bare shifting sands. The long spit of marsh which stretches along in the direction of the mouth and lies between the main river-channel and the sand-dunes on the N.E. side affords an admirable example (cf. Fig. 15). The main body of this marsh-spit is composed of hummocky ground, bearing *Salicornia radicans* and *Obione portulacoides* in profusion, together with a scattering of *Glyceria maritima*, *Suæda maritima*, and other halophytes on its more settled portions. This marsh-spit is accompanied along the whole stretch of its duneward flank by a broad sandy belt, often 50 or more feet across, of dwarf plants which are doubtless a peculiar form of *Salicornia radicans* (A—A, Fig. 15), whilst its other flank (directed towards the main channel) is bordered by a corresponding zone of the form of *Salicornia herbacea* which is sometimes distinguished as *S. ramosissima* (the hatching B—B, Fig. 15). This however is rooted in mud or muddy sand, black in colour.

Taking first the *S. radicans* zone on the duneward flank. This consists of little prostrate plants, sparsely scattered at the rate of about one per square yard. These plants, though indistinguishable from *S. radicans* in its first year, have the peculiarity of behaving as annuals, and, although they flower regularly, have been observed on several occasions to decay without ripening seed[1]. Evidently they are the pioneers of the phanerogamic vegetation and under their influence the sand is being gradually fixed. Our data prove that at many places along this zone extensive groups of permanent plants of *S. radicans* have arisen, doubtless by the survival of the dwarf annual variety in favoured places. In this way several acres of ground have acquired during the last few years a permanent covering of tussocks of *S. radicans* which quickly accrete sand-hummocks and grow with luxuriance. These promoted plants are quickly joined by Obione and later by Glyceria. The secondary phases of colonisation, however, are less strikingly shewn here than in other regions of the marsh, to be alluded to below. At present the conditions favour the primary phase, whilst secondary colonisation and consolidation appear to be in relative suspense.

On the side towards the channel (B—B, Fig. 15) the belt consists, as we said, of *S. ramosissima*; erect plants so closely grown as almost to touch one another. These of course are annuals and the zone is renewed each year. The ground they occupy is rich in humus and the evidence shews that at places the territory occupied has undergone considerable extensions. There is no tendency for the ground to become hummocky, nor—apart from *Rhizoclonium*—do other plants establish a footing. It seems evident that two different types of colonisation are in progress on the two sides of this marsh-spit and that these types should correspond to incipient phases of distinct associations. The further history of the *Salicornia radicans*-hummocks is epitomised below.

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[1] This year, however, they are seeding copiously.

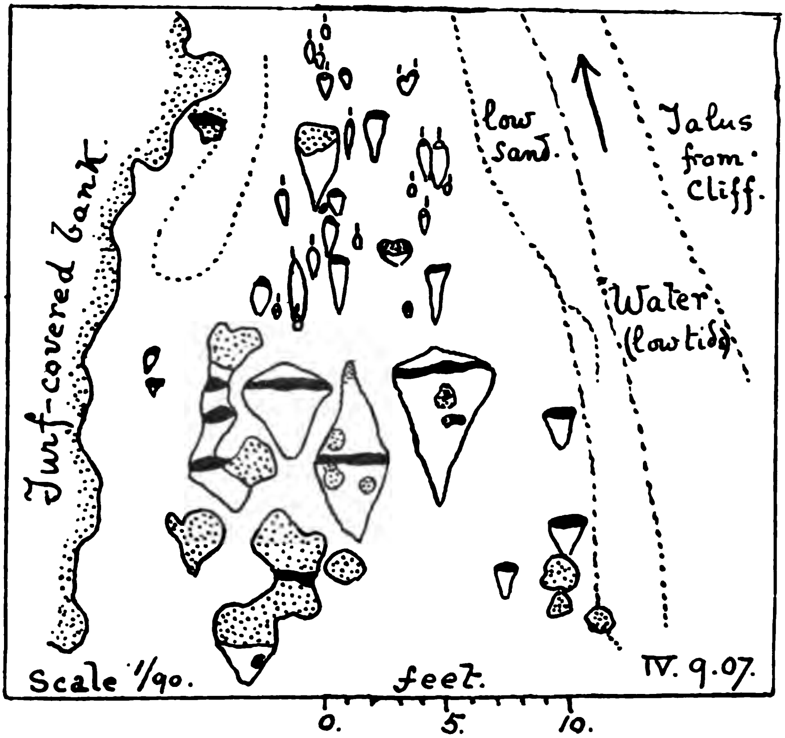

Fig. 16. Map shewing colonisation of a sand-bank in the bed of a channel. The rhomboidal figures are the outlines of sand hummocks collected since 1903 by plants of *Salicornia radicans* and *S. herbacea*. The black transverse belts mark the *S. radicans*, whilst the position of *S. herbacea* is marked by short vertical strokes. The hummocks accumulated by the latter are relatively small. The shading marks areas (hummocks) further colonised by *Glyceria maritima* and *Suæda maritima*. These two plants do not appear to settle directly on the sand-bank itself. The arrow points down stream. Scale $\frac{1}{90}$.

In view of so much evidence of advancing development it seemed desirable to construct a more detailed survey of this portion of the marsh than could be obtained by a mere revision of the general map of 1904. For this purpose one of the old perpendiculars (forming the axis of the spit) from the original base-line was revived, and in relation to this the areas of interest were mapped by the "gridiron" method on a scale of $\frac{1}{80}$. By means of a series of long transects thrown across the perpendicular all strategic points can now be kept under close observation.

To complete the history of the hummocks it is necessary to turn to one of the sand-banks in the bed of the principal channel in the Farm area (known as "Stream B").[1] In September, 1903, when this sand-bank first came under observation, it bore nothing but a thin scattering of small isolated plants of *Salicornia radicans* and *herbacea*. Since that date colonisation has advanced rapidly (see Fig. 16). The *S. radicans* plants, being perennial, have gone on collecting sand from the channel as the sand-laden tide rushed over them, till they have grown into hummocks eight or ten inches in height, and three to five feet in length. These hummocks, which tend to run together into hummock-systems (as at the left-hand bottom corner of Fig. 16), have undergone secondary colonisation by *Obione, Glyceria* and *Suæda*. The more advanced amongst these covered hummocks are to all intents and purposes identical with the Grass-Suæda hillocks that form so considerable a feature upon the more stable portions of the Farm area. Inspection of the adjacent parts of the covered marsh shews that much of this tract has developed in the same way. The sand-bank, as it was in April, 1907, is represented in the grid map reproduced in the accompanying Fig. 16. The grass-covered system of hummocks on the left is quite ready for incorporation in the settled marsh so soon as the stream abandons the sand-bank in the progress of its meandering.

The rapid growth revealed by this sand-bank—essentially a concise epitome of what is happening on the spit—depends doubtless on the favourable position which it occupies in the bed of a channel up which the sand-laden tide rushes with considerable velocity. The extension of the *S. radicans* in belts *at right-angles to the direction of flow* is a striking feature, the physiological significance of which stands in need of elucidation. Of its efficiency as a sand collector there can be no question. The whole mechanism, including the transverse position of the belt, closely resembles the collecting of sand on a sand-dune by *Psamma*, if water-carriage be substituted for wind-transport. The map (Fig. 16) brings out another point, *viz.*, the relative ineffectiveness of the annual *Salicornia herbacea* in this type of marsh-building. For these plants have no lateral extension nor do they recur from year to year at the same spots. The hummocks which they attach are very small.

---

[1] This channel forms the axis of the complex system of water-courses depicted on the left of Fig. 15.

Hummock-complexes originating in the way described may remain as such, or more frequently, *Salicornia herbacea* settles in the depressions between, developing in some cases into apple-green channels, whilst in others, probably where the soil is less permeable, the hummocks appear to be gradually embedded, so that the ground is levelled up. The details of these further stages of development have not, however, been fully worked out as yet.

Of the mode of origin of the very characteristic red Salicornia-flats or "crimson plains" there are no data available, as undoubted developmental stages have not been detected. It is possible, no doubt, that the zones of *Salicornia ramosissima* (described on p. 250) represent an early phase of this association, but it is premature to venture on a definite opinion.

OTHER WORK.

In connection with the developmental studies outlined above, a beginning was made, by the Chemical Section, of an investigation into the nature of the progressive changes which the soils undergo in the successive phases of colonisation. The bacteriology of the soils is also receiving attention.

In the Physiological Section the work upon transpiration and osmotic pressure was continued. As regards the latter the young seedlings afford by far the most convenient material; and as both Salicornia and Suæda can be readily grown in water-cultures it seems probable that this method will be the most useful one to adopt.

For the first time since the inception of the work a photographic specialist was able to devote his undivided energies to photographic studies on the marsh. A dark room was fitted up at the Laboratory by Dr. Somerville Hastings who developed more than a hundred negatives illustrating various branches of the investigation. Colour photography was represented by Dr. Kenneth Mees, and his results will be awaited with interest.

As in former years the local population received us with every consideration and in a variety of ways gave evidence of the cordiality and kindliness of their feelings towards the party.

F. W. OLIVER.

R. MADLBY, Steam Printer, 151, Whitfield Street, Fitzroy Square, W.

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VOL. VI., No. 10. DECEMBER 31ST, 1907.

THE NEW PHYTOLOGIST

A BRITISH BOTANICAL JOURNAL,

EDITED BY A. G. TANSLEY, M.A., F.L.S.

UNIVERSITY LECTURER IN BOTANY, CAMBRIDGE.

Contents:

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NOTES ON RECENT PHYSIOLOGICAL LITERATURE.
II.—ILLUMINATION AND VEGETATION ... ... *F.F.B.*

THE ORIGIN OF TRIPLE FUSION: A SUGGESTION. [TEXT-FIG. 17] - - - - - - - - - *E. M. Berridge.*

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NEW PHYTOLOGIST.

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LECTURES ON THE EVOLUTION OF THE FILICINEAN VASCULAR SYSTEM.[1]

By A. G. TANSLEY, M.A.

University Lecturer in Botany, Cambridge.

LECTURE VIII.

THE OSMUNDACEÆ AND OPHIOGLOSSALES.

[FIGS. 81—95.]

WE have now completed our task of tracing the evolution of the vascular system in the Filicinean phylum from the simple protostelic forms found in the Hymenophyllaceæ and Gleicheniaceæ to the most complicated dictyostelic and polycyclic types such as we find in the most advanced Marattiaceæ.

In so doing we have omitted the consideration of two important families or groups (one undoubtedly Filicinean, and the other shewing several Filicinean features) because they stand rather apart from the main lines of anatomical evolution so characteristic of the great majority of the Ferns. To these we must now devote some attention.

OSMUNDACEÆ.

Undoubted representatives of this very old family are known from the Jurassic and Rhætic, while certain Palæozoic forms show a considerable resemblance to the family type. The Osmundaceæ are now represented by two genera, and are distinctly isolated in several respects; in the development and structure of the sporangia, in the structure of the prothallus, and even more markedly in the anatomy of the stem. The sporangia stand closest to those of the Botryopterideæ, and the structure of the vascular system of the stem in some existing forms recalls that of *Zygopteris*, particularly of *Z. corrugata* (Fig. 5), while quite recent discoveries of Kidston and Gwynne-Vaughan ('07)[1] make the connexion with Botryopterideæ even plainer, by revealing the existence in *Osmundites* of types of structure clearly connecting the recent Osmundaceæ with the simplest form of Botryopteridean stele, such as that of Renault's *Grammatopteris Rigolottii*. It would thus be most natural to deal with the Osmundaceæ immediately after the Botryopterideæ, and at the beginning of the series of living Ferns. This course was not adopted in the present lectures partly because the line of evolution in the Osmundaceæ stands, as has been said, apart from that of the great majority of living ferns and did not form a suitable introduction to the bulk of our subject matter, and partly because some of the phenomena displayed have led to the propounding of a view that the Osmundaceous series of types really represents a reduction-series from a dictyostelic form, instead of a progressive series starting from a simple protostelic form. This view could not be discussed adequately except in the light of our knowledge of the anatomy of the other Ferns.

---

[1] A Course of Advanced Lectures in Botany given for the University of London at University College in the Lent Term, 1907.

We will begin with a consideration of the two living genera *Osmunda* and *Todea*, which agree closely in the leading features of their structure.

The stem is upright or obliquely ascending, in some cases (*Todea barbara*) rising some feet above the ground like a small tree-fern. Usually, however, it is quite buried in the soil. The diameter of the stem is very greatly increased by the thick, woody, overlapping leaf-bases, which completely surround it, and also by the numerous roots. The phyllotaxy is a complicated spiral such as $\frac{8}{21}$.

A transverse section of the central cylinder in the majority of species (Fig. 81) shows a circle of xylem strands of different shapes (some U-shaped with the concavity directed inwards, and some more or less oval or circular in cross-section) separated from one another by rays of parenchyma, while the whole is surrounded by a complete ring of parenchyma (mesocycle) and phloem, bounded externally by pericycle and endodermis.

The phloem characteristically forms wedge-shaped projections into the rays. At certain points, outside the ordinary vertically running sieve-tubes, and sometimes interrupting the circle of these, are tangentially elongated cells which have the structure of normal sieve-tubes. It seems that these are best regarded as part of the phloem, the orientation of the elements being disturbed by the exit of the leaf-traces, a disturbance which also affects the pericyclic cells in the vicinity. Faull ('01) regarded them as part of the protophloem, but Seward and Ford ('03) show that in *Todea* they are developed *after* the large sieve-tubes lying nearer the xylem. The centre of the stele is occupied by a parenchymatous pith which in some species contains strands of sclerenchyma. Each strand of xylem consists of a solid mass of scalariform tracheæ without internal parenchyma. The spiral protoxylems are situated in the concavity of the U-shaped strands, abutting on the parenchyma, while the strands of oval or circular cross-section are mesarch or destitute of protoxylem.

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[1] Published since these lectures were delivered, and partly still unpublished.

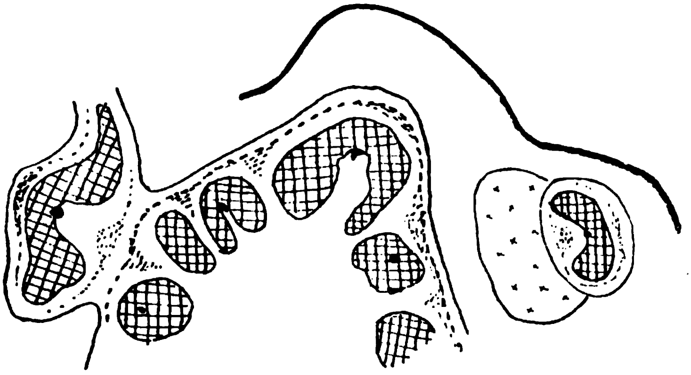

Fig. 81. *Todea barbara.* Diagram of part of stem in transverse section, with two leaf-traces. The varying shapes of the xylem strands and the varying positions of the protoxylems are shown. From Seward and Ford.

Thus the construction of the stele differs very markedly from that of any of the Ferns with which we have become familiar in the course of these lectures.

The U-shaped strands are those which give off the leaf-traces. The outer part, connecting the limbs of the U, separates off as a slightly curved arc, and becomes surrounded by phloem, that which covers the convexity of the trace being continuous with the external phloem of the stele below, while that which lines the concavity is continuous with the external phloem of the stele above, in the same vertical line (Fig. 82). The limbs of the U remain behind in the stele, and pass on upwards to join similar strands coming from other nodes, eventually forming the leaf-traces of higher nodes. In *Osmunda regalis* according to Zenetti (Fig. 83) the left-hand strand (the cylinder being

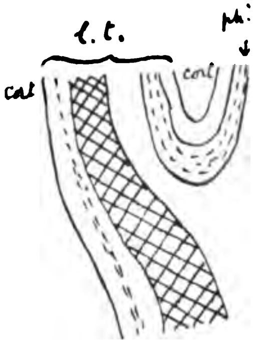

Fig. 82. Diagram illustrating connexion of internal phloem of leaf-trace with phloem of stele, as seen in radial section of the stele at the point of departure of a trace. *l.t.*, leaf-trace; *cort.*, cortex; *ph.*, external phloem of stele above departure of trace. From Seward and Ford.

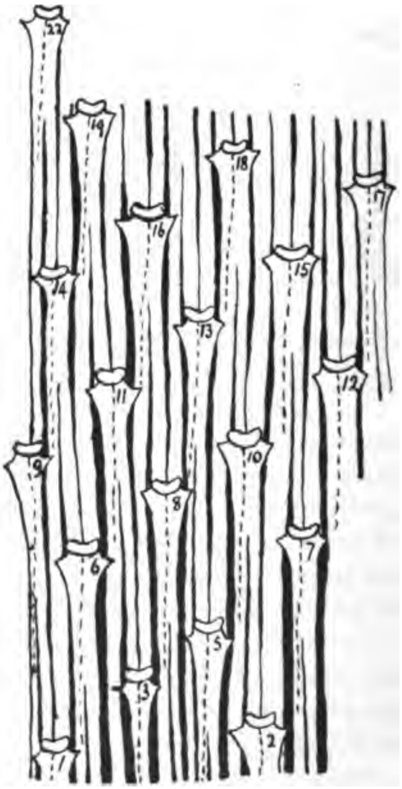

Fig. 83. *Osmunda regalis*. Diagram illustrating the course of the xylem strands of the stele. The leaf traces are numbered from below upwards. Leaf-gaps black, protoxylems dotted. After Zenetti.

regarded from without) forms the right-hand portion of the eighth leaf-trace above, while the right-hand strand forms the left-hand portion of the thirteenth leaf-trace above. When one of these oval strands joins a similar strand from another node it closes a leaf-gap, and these strands therefore correspond with the "compensation strands" of dicotyledons. Phylogenetically, of course, they are the cauline parts of the original cylinder.

In some Osmundaceæ (e.g., *O. regalis*) the leaf-gaps (which only affect the xylem of the cylinder) are extremely long, being continued upwards for eighteen internodes above the exit of the trace[1] (Fig. 83). It is this great length, and the consequent overlapping of many gaps, which gives rise to the long, independent course of the "compensation-strands." In the species with shorter gaps the strands fuse with their neighbours so much the sooner.

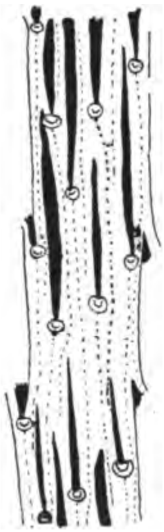

Fig. 84. *Todea barbara.* Diagram of course of xylem strands in the stele. Leaf-gaps black, protoxylems dotted. From Seward and Ford.

The single protoxylem in the concavity of each leaf-trace is continued downwards into the stem as the protoxylem already mentioned in the concavity of each U-shaped strand of the stem-cylinder. Traced downwards the two arms of the U approach and fuse, so as to enclose an island of parenchyma containing a protoxylem group, enclosed in a solid mass of xylem. The xylem-strand thus becomes mesarch and circular or oval in section. At a lower level this oval strand divides into two (the two compensation strands, which—traced upwards—here fuse and close a leaf-gap). The protoxylem enters one of these two strands and soon dies out, about five internodes below the entry of the leaf-trace in *O. regalis*. It thus has no connexion with that of either of the leaf-traces entering below, on which the two forks respectively insert themselves. It is of interest to note that in *Todea barbara*, where the leaf-gaps are comparatively short (Fig. 84), each protoxylem strand can be traced down into the neighbourhood of the eighth leaf-trace below, where it dies out in one of the compensation-strands connected with that leaf, while in *Osmunda regalis*, where the leaf-gaps are very long, there is an independent xylem-strand running the same course (see above).

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[1] According to Lachmann ('89) Plate V., Fig. 1), the phyllotaxy is sometimes $\frac{5}{13}$, and in such a case of course the leaf-gap cannot extend for more than thirteen internodes.

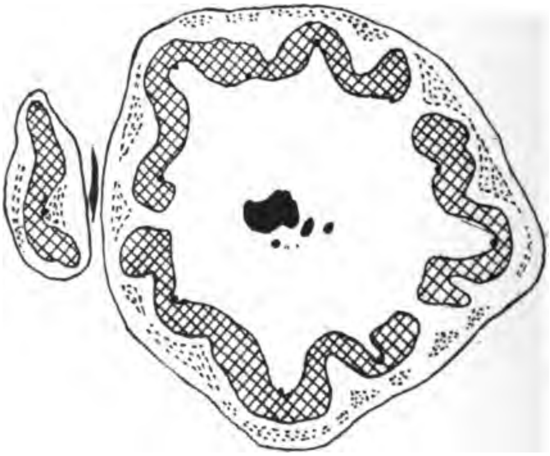

Fig. 85. *Todea barbara*. Stele in transverse section showing relative lateral continuity of xylem. cf. Fig. 84. From Seward and Ford.

Given the same phyllotactic spiral, with the same inclination to the horizon, the longer the leaf-gaps the more will appear in any given transverse section. If the phyllotaxy be simpler or the spiral runs at a steeper angle (*i.e.*, if the leaves are less crowded) there will be fewer gaps in transverse section, and if the gaps are shorter, fewer still. In *Todea barbara* and *T. superba* the gaps are comparatively short (Fig. 84) and consequently the xylem of the stele, as seen in transverse section, may consist of only two or three undulating bands of xylem (separated by as many gaps), in each of which several protoxylems have their course (Figs. 85 and 86).

In *Osmundites Dunlopi*, a form recently described by Kidston and Gwynne-Vaughan ('07) from the Jurassic rocks of New Zealand, the xylem-cylinder is nearly, or perhaps quite, laterally continuous,

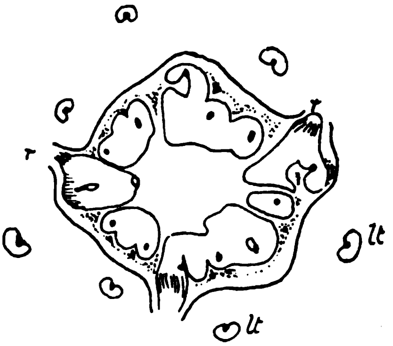

Fig. 86. *Todea superba.* Transverse section of stele showing relative lateral continuity of xylem. *l.t.*, leaf-trace; *r.*, root. From Seward and Ford.

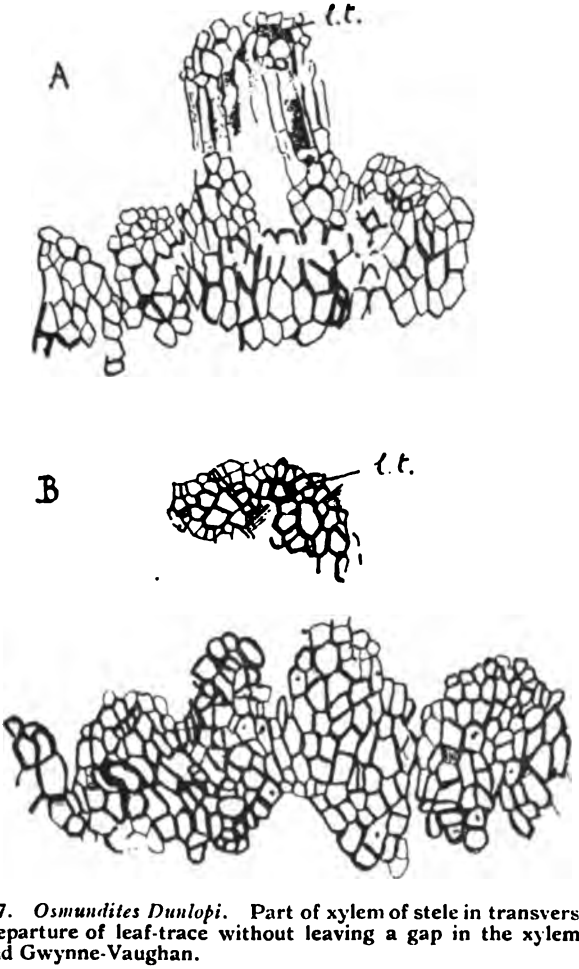

Fig. 87. *Osmundites Dunlopi.* Part of xylem of stele in transverse section showing departure of leaf-trace without leaving a gap in the xylem. From Kidston and Gwynne-Vaughan.

the leaf-traces departing from its outer surface without making any gap in the cylinder (Fig. 87). Apparently this is sometimes also the case in *T. superba* (Fig. 86).

In *Osmunda cinnamomea*, on the other hand, we meet with a more complicated type of structure than that characteristic of the central forms of the family. In this plant Faull ('01) discovered an internal endodermis throughout the stem, separating the pith from the xylem, and, in addition to this, locally developed internal phloem, consisting of quite normal sieve-tubes between the internal endodermis and the xylem. This internal phloem sometimes forms a continuous ring, but often occurs in more or less detached groups. It occurs only in the neighbourhood of the branching of the stem, both above and below the actual fork (Fig. 88). At the branching there is often, though not always, a complete break or gap in the vascular cylinder, placing the pith in continuity with the cortex, the internal endodermis in continuity with the external, and the internal with the external phloem. In other cases there is a less extensive interruption of the tissues, the central portion of the pith below the fork being continuous with the cortical ground-tissue above, but the inner and outer endodermis not coming into connexion. In rare cases there is a union of internal and external phloem also through the xylem leaf-gaps.

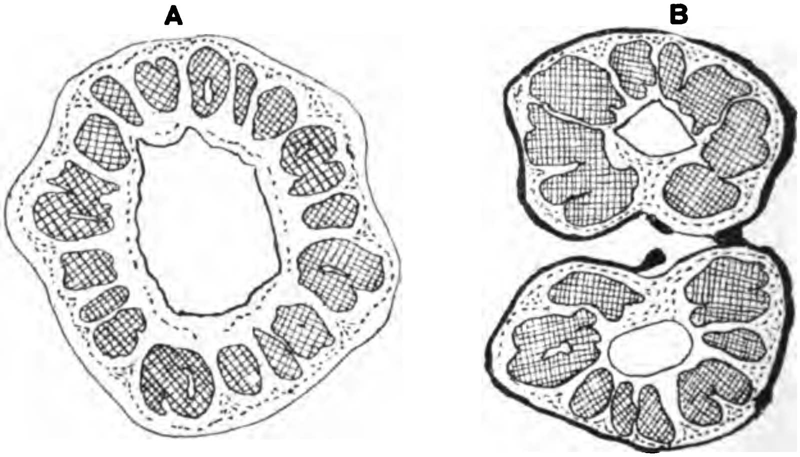

Fig. 88. *Osmunda cinnamomea.* A.—Transverse section of stele showing almost continuous internal phloem and endodermis. B.—Steles of the two branches of a stem showing the "subsidence" of the external phloems through the xylem-branch-gaps, continuous with the internal phloem of the parent axis below. After Faull.

In the adult stem of *Todea hymenophylloides*, Seward and Ford also found an internal endodermis surrounding a sclerenchymatous pith. This internal endodermis does not, however, occur in the stems of very young plants (Fig. 89), and no internal phloem was found anywhere.

In *Osmundites skidegatensis* Penhallow (Fig. 90), the type of structure is like that of *Osmunda cinnamomea*, except that the internal phloem of the stele is constant, and is continuous with the external phloem through each leaf-gap, while the whole vascular cylinder is interrupted at the leaf-gaps, the pith coming into connexion with the cortex, so that we have a true dictyostele produced, differing from the ordinary dictyostelic type of the higher Leptosporangiate Ferns by the extreme narrowness of the gaps, by the characteristic shape and course of the xylem-strands and by the other anatomical features peculiar to the Osmundaceæ.

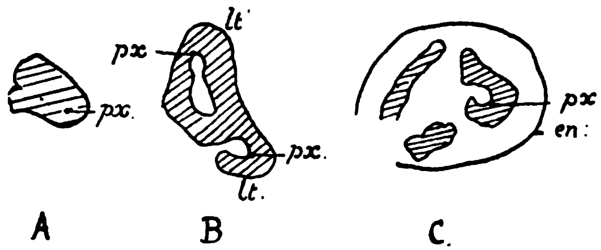

Fig. 89. *Todea hymenophylloides.* Successive stages in the evolution of the stele of the young plant. A.—Stage with protostelic solid xylem. B.—Stele with pith showing "protostelic" departure of leaf-trace. C.—Xylem cylinder showing three distinct strands. From Seward and Ford.

It is thus obvious that we have, in the Osmundaceæ, a continuous series of types of stem-structure, beginning with such a form as *Osmundites Dunlopi* (represented also in the first-formed stems of living types—Fig. 89, B) and ending with the complex structure of *O. skidegatensis.* The considerable resemblance between the simplest form of Osmundaceous stele, with continuous xylem, and such a form as *Zygopteris corrugata* is striking enough, while the apparent primitiveness of the Osmundaceous sporangium and its resemblance to the Botryopteridean type renders the hypothesis of a real phylogenetic connexion between the two types of stele decidely probable.

This probability is, however, very greatly increased by the quite recent, and as yet unpublished, discovery by Kidston and Gwynne-Vaughan of undoubted Osmundaceous stems connecting the type of *O. Dunlopi* with such a form as Renault's *Grammatopteris Rigolottii* (see p. 55). The evidence for regarding the Osmundaceous series as an ascending one has thus become all but overwhelming.

On the other hand Faull and Jeffrey have contended that the state of things seen in *O. cinnamomea*, in which internal phloem exists in the neighbourhood of the forks of the stem, is more primitive than the typical structure of, for instance, *O. regalis*, and represents a degraded form of the "amphiphloic siphonostele," which is supposed to have been the ancestral type. From the type of *O. cinnamomea* such a form as *O. regalis* is supposed to have arisen by the complete disappearance of the vestigial internal phloem and of the internal endodermis, and the complete shutting off of the pith from the cortex. The discovery of *O. skidegatensis* would seem to have furnished these authors with their hypothetical ancestral type from which to derive *O. cinnamomea*.

The arguments that appear to me to tell rather in favour of this view may be briefly stated as follows. Ferns which have a continuous internal endodermis throughout the stem and no internal phloem are decidely rare. We have such a case, however, in the Gleicheniaceous genus *Platyzoma* (pp. 140—143), and the stele of this plant also resembles that of the Osmundaceæ in having no leaf-gaps putting the cortex in connexion with the pith, the leaf-traces departing from the outer surface of the xylem-cylinder somewhat as in the simpler Osmundaceous types. There is good reason for considering *Platyzoma* as an instance of reduction. In the Vittarias and Antrophyums, also, we apparently have a reduction-series culminating in the complete disappearance of internal phloem, while in some forms it remains only in the neighbourhood of the leaf-gaps (pp. 192—3). *Schizæa* and the Ophioglossaceæ might also be cited

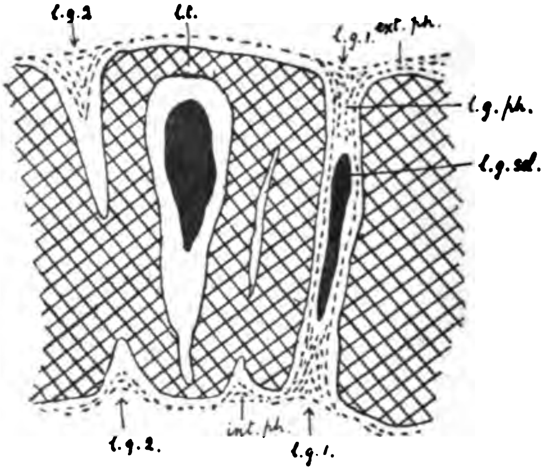

Fig. 90. *Osmundites skidegatensis*. Diagram of part of stele. *l.g.*1., leaf-gap with phloem continuous. *l.g.*2., leaf-gap with xylem closed. *l.t.*, leaf-trace not yet detached. After Kidston and Gwynne-Vaughan.

in this connexion, but though they may conceivably have been derived from "amphiphloic" forms there is no actual evidence that they ever possessed internal phloem.

If we do not accept Faull's view of *Osmunda cinnamomea* as a degenerate type we seem bound to raise the question of why the internal phloem has arisen in the neighbourhood of the branching of the stem. It may have "crept round" the edges of the branch-gaps, or have "subsided" into them, but the use of such a phenomenon must remain a mystery. We may remember however that we found a somewhat similar difficulty in explaining the phloem-pockets of Gleicheniaceæ, and there is little reason to suppose that these are reduction-phenomena. The solution of such problems may not improbably be found when we know more of the actual function of phloem.

One of the strongest arguments against Faull's view is undoubtedly that which has been advanced by Boodle, Seward and Ford, Chandler, and Kidston and Gwynne-Vaughan, namely the entire absence of any evidence of the existence of internal phloem in any of the young plants that have been examined.

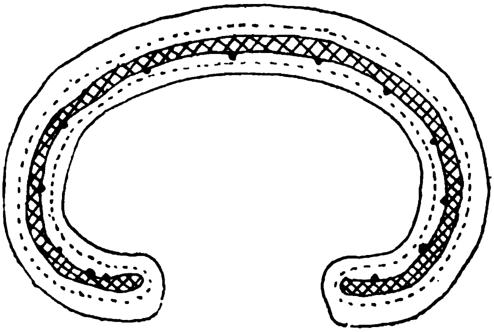

Fig. 91. Diagram of transverse section of an Osmundaceous petiolar strand.

Another significant fact is the absence of any sign of reduction in the leaf-trace. We have seen good reason to believe that in the main Leptosporangiate series the stele passed through the *Lindsaya*-stage on its way from the protostelic to the solenostelic condition, and that the continuous internal phloem of the stele is of value as giving a more adequate attachment to the phloem of the concavity of the leaf-trace. In the Osmundaceous leaf-trace we have phloem completely lining both the convexity and the concavity (Fig. 91) and yet the internal phloem of the trace is in connexion only with the external phloem of the stem. On the general principle of basipetal evolution of vascular structure we should regard this as a more primitive condition than that in which the internal phloem of the petiolar strand is attached to internal phloem of the stem-stele. But on Faull's view we should have to suppose that the internal cauline phloem had completely disappeared while the internal phloem of the trace remained intact.

It should be pointed out that even in *O. skidegatensis* the phloem lining the concavity of the leaf-trace is not directly continuous in the radial plane with the internal phloem of the stem-stele. Traced downwards it dies out, in the concavity of the U-shaped strand of xylem, below the point of insertion of the trace. It is the external phloem of the stele, on the right and left of the leaf-gap which becomes continuous, at a higher level, through the gap with the internal phloem of the stele. Here we have, *pace* Faull's statement that the Osmundaceous stele "is neither primitive nor anomalous among the Filicales," a character which is certainly quite exceptional among the Ferns, and which seems to be connected with the "protostelic" mode of departure of the leaf-traces. In spite of the breaking up of the xylem of the Osmundaceous stele into separate strands, this "protostelic" mode of departure is essentially maintained in the most advanced forms, inasmuch as the leaf-trace always departs from the outer face, and does not "take away" a complete segment of the cylinder. For these reasons the suggestion of Kidston and Gwynne-Vaughan that the internal phloem and endodermis of *O. cinnamomea* should, perhaps, be regarded as "cladosiphonic," in the sense that their development started from the branch-gaps, not from the leaf-gaps, is certainly to be regarded as a plausible one. And for all we know to the contrary the stele of *O. skidegatensis* may represent a higher phase of the same type, in which the internal and external phloem have become secondarily continuous through the leaf-gaps, as they are occasionally in *O. cinnamomea*. It is no doubt conceivable that *O. skidegatensis* is reduced from a normal dictyostelic type, in which the leaf-traces have secondarily come to depart from the outer face of the xylem cylinder, their internal phloem has ceased to be connected with the internal phloem of the stem, and the leaf-gaps have become very narrow. Some such process of reduction as this has very likely occurred, as we have already said, in *Platyzoma*. But when we consider the palæontological evidence connecting Osmundaceæ with Botryopterideæ, as well as the other considerations given above, such a hypothesis becomes distinctly unlikely.

Our general conclusion must be then, that the theory of the typical Osmundaceous stele as a reduced type of structure, a theory for which there was never a really strong case, has been rendered much less probable by the work of Gwynne-Vaughan and Kidston, and that while it is conceivable that the type of structure seen in *Osmunda cinnamomea* has been reduced from the type of *O. skidegatensis*, no sufficient reason has been assigned for such a reduction, any more than for the supposed further reduction to the type of *O. regalis*. Certainly the appearance of such a form as *O. cinnamomea* is by no means completely explained, but on the whole fewer difficulties are involved by regarding it as a progressive than as a retrogressive type.

OPHIOGLOSSALES.

There is no need to discuss in this place the various affinities that have been suggested for this very isolated group of plants. The outstanding morphological character of the group is of course the forking of the leaf into a fertile (ventral, adaxial) and a sterile (dorsal, abaxial) limb. The general feature of the group which interests us most from the anatomical point of view is their megaphylly and their possession of a hollow vascular cylinder which is broken by the departure of leaf-traces (Fig. 92). It will only be necessary to treat the leading features of the group quite shortly.

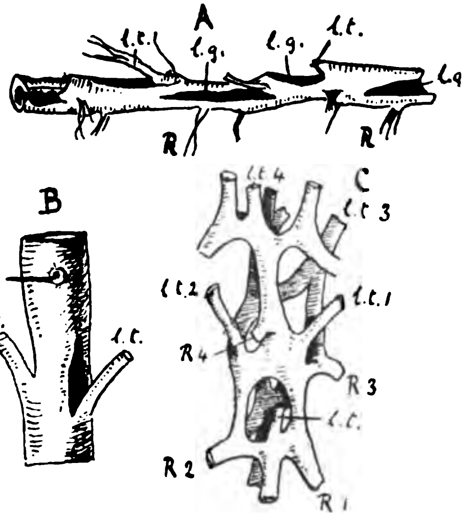

Fig. 92. Steles of Ophioglossales. A.—*Helminthostachys*, after Farmer and Freeman. B.—*Botrychium Lunaria*. C.—*Ophioglossum vulgatum*, after Holle. *l.t.*, leaf-trace; *l.g.*, leaf-gap; *R.*, Root stele.

It is most convenient to begin with the monotypic genus *Helminthostachys*, confined to the Indo-Malayan region, and with the most complicated leaf-segmentation found in the group.

The rhizome is subterranean, creeping and dorsiventral, bearing two rows of leaves on the upper surface, and numerous roots on the lateral and ventral faces. It contains a hollow cylindrical vascular skeleton (Fig. 92, A, Fig 93), with a ground tissue pith continuous with the cortex through the leaf-gaps, but no internal phloem. An internal endodermis is present which is irregular and often interrupted, suggesting reduction. The xylem is mesarch, with spiral protoxylem, and the tracheids of the metaxylem possess highly developed bordered pits. The leaf-trace departs as a single curved mesarch strand, and leaves a well-marked elongated leaf-gap. The trace splits almost at once into strands symmetrical about the vertical plane, and each of these again divides into two, so that four strands, which are diagonally arranged and have crescentic endarch xylems enter the petiole. Each of these again bifurcates, giving rise to four diagonal pairs of bundles, the members of each pair being turned towards one another (Fig. 94). The eight bundles become equidistant and undergo some further splitting, increasing in number to ten or twelve. The bundle representing one free end of the typical leaf-trace curve becomes specially large, and gradually sinks into the centre of the petiole, where it turns round so that its protoxylem faces adaxially (Gwynne-Vaughan '05). Branches from this internal strand pass out to the pinnæ. The vascular supply of the fertile spike is derived from the two middle strands on the upper

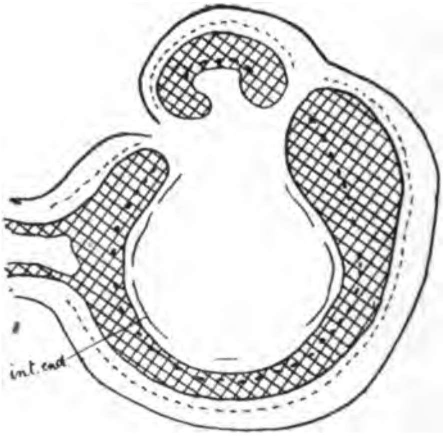

Fig. 93. *Helminthostachys zeylanica.* Diagram of transverse section of stele showing departure of leaf-trace (above) and root-stele (to left).

(adaxial) side of the petiolar circle, and also from the large central strand whose origin has been described. The venation of the frond is dichotomous, and taken in conjunction with the repeated dichotomy of the leaf-trace strands, and with the partially dichotomous branching of the frond, suggests a primitive feature.

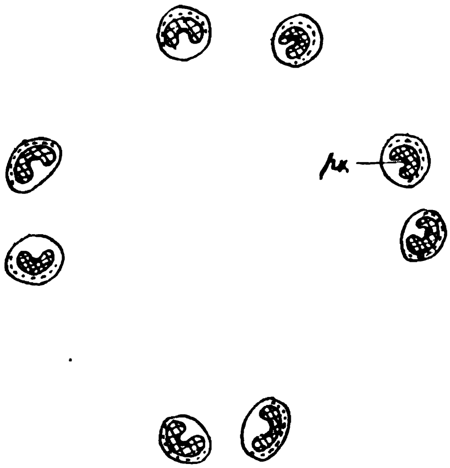

Fig. 94. *Helminthostachys.* Eight bundles in four pairs near base of petiole. The ventral (adaxial) side of the petiole comes between the bottom and left-hand pair, these pairs representing the free ends of the petiolar curve.

The vascular structure of the genus *Botrychium*, which contains several species scattered over the world, resembles that of *Helminthostachys* in a quite general way. Thus the stem contains a hollow cylinder of xylem, with a parenchymatous pith, and with external phloem, pericycle and endodermis. In details there are great differences. The xylem is endarch; the metaxylem tracheids, which have highly developed bordered pits, are radially seriated, and these series are interspersed with medullary rays one cell thick. The vascular cylinder is added to by a cambium just like that of a dicotyledon, except that no new elements are added to the phloem. In the stem of the young plant there is an internal endodermis surrounding the pith; this dies out when traced upwards.

The leaf-trace again consists of a single strand which forks at the base of the petiole, and eventually a circle of strands is formed which are concentrically organised, but with a tendency, in some species, to collateral structure. The supply of the fertile spike appears to take place as in *Helminthostachys*, but here no central bundle has been found in the petiole. The venation is like that of *Helminthostachys.*

The species of *Ophioglossum* have closely crowded simple or dichotomous leaves and the vascular cylinder of the stem bears the same sort of relation to that of *Helminthostachys* or *Botrychium* that a simple dictyostele bears to a solenostele in the Leptosporangiate Ferns, *i.e.*, the leaf-gaps overlap, so that in transverse section the stem-cylinder appears as a number of collateral bundles arranged in a ring (Fig. 95).[1] The leaf-trace, as in the other genera, consists of a single strand which starts from the base of a leaf-gap (Fig. 92, C), and apparently forks as in the other genera. The leaf-venation is reticulate.

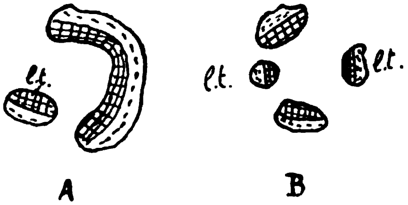

Fig. 95. *Ophioglossum vulgatum*. Diagrams of transverse sections of stele; A showing one, B two overlapping leaf-gaps.

The roots of *Helminthostachys* are usually hexarch (tetrarch to heptarch), of *Botrychium* triarch or tetrarch, but diarch in *B. Lunaria*, with occasional monarchy apparently by reduction of one protoxylem and fusion of the two phloems. In *Ophioglossum* the roots are usually diarch or monarch as in *Botrychium Lunaria*, though in some species triarch or even tetrarch.

Though the three genera of Ophioglossales probably have no very near connexion with one another in descent, it seems that the most likely view of their relationship, so far as anatomy is concerned, is to regard the three types as on the whole representing a reduction-series, starting with *Helminthostachys*, which itself shows distinct signs of reduction in its incomplete and irregular internal endodermis. *Botrychium* may in some respects be regarded as still further reduced, *e.g.*, in the complete loss of the internal endodermis in the adult plant, and in its endarchy, while its possession of a cambium may be a fresh progressive development. *Ophioglossum* is certainly more advanced than the other two from the point of view of its "dictyostelic" structure. Its actual vascular strands suggest reduction, as does the symmetry of the root-stele.

On the whole, in fact, so far as anatomy is concerned, it looks as if evolution had progressed within the group more from the type of *Helminthostachys* to that of *Ophioglossum* than in the other direction, though the individual genera are too peculiar and isolated to make it reasonable to lay very much stress on the point.

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[1] In some cases, however, the leaf-gaps do not overlap.

There is no evidence of internal phloem in any member of the group, and the type of *Helminthostachys* is probably derived from that of a mesarch protostele which has acquired a ground-tissue pith. This view leaves us free to relate the Ophioglossales to primitive Ferns, Cycadofilices, Sphenophyllales or Lycopods, or to the common ancestors of all these groups. The line of evolution within the group, from the meagre evidence afforded by the existing types, is to some extent parallel with that of the Ferns, but in other respects nearer the Cycadofilices. The marked megaphylly of the Ophioglossales also tends, of course, on the views expressed at the beginning of the present course of lectures, to relate them to one or both of these last-mentioned groups rather than to the microphyllous forms. Nevertheless, the morphological resemblance of the sporophylls to the *Sphenophyllum-Psilotum* type cannot be entirely ignored, and the net result of a consideration of the Ophioglossales from all points of view, is a strengthening of the tendency to relate all these groups,[1] so widely divergent at the present day, to some very remote, but essentially megaphyllous ancestor.

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[1] With the possible exception of the Lycopods.

NOTES ON RECENT PHYSIOLOGICAL LITERATURE

II.—ILLUMINATION AND VEGETATION.

J. Wiesner.—Der Lichtgenuss der Pflanzen, 322 and viii. pp., with twenty-five figures. Leipzig, 1907.

FOR green vegetation illumination of some sort is clearly essential. When we come to make a scientific study of the relation between the intensity of this illumination and the vigour of vegetation we find that the matter is by no means so simple as might be anticipated.

A mere estimation of the intensity of natural illumination in any given habitat is by no means easy, while the working out of the effects of light upon all the separate vital processes of the plant has provided occupation already for many generations of investigators, without finality being reached. The algebraical summation of these effects to give the numerical relation between the illumination and the vigour of any one plant, *as a whole*, is as yet quite beyond us.

Preliminarily, this last relation may be approached *empirically* and to this aspect of our problem no one has devoted more work than Professor Wiesner. In the last fifteen years he has published a score of papers on the subject of *Lichtgenuss*, and just recently he has embodied the essentials of his work in the very readable book which has suggested this article.

I.

Let us first consider the illumination of the earth's surface, and methods of measuring it.

The sun illumines our planet partly by its direct rays which penetrate through our atmosphere and partly, indirectly, by the scattered diffused light radiating in all directions from the heavens. This light is a temporary deduction from the sun's direct rays by the atmosphere, not entirely lost to us, but eventually straggling down in the form of a mild diffuse radiance. When direct insolation is blotted out by clouds or mist, diffuse light, provides a considerable light-intensity. Both these components of our total light go through a diurnal and annual rhythm of intensity, and the precise form of the curves expressing these variations is different for every degree of latitude from equator to pole. Different parts of the earth have thus a special climate as regards light just as in regard to temperature.

Were clouds and mist absent, or uniform in their occurrence the light-climate of places could be calculated from the known elevation of the sun at different hours and the absorbing and scattering power of the different thicknesses of atmosphere superposed upon places at different levels above the sea. Clouds and mists being as wayward as they are, the climatic intensity of light in different places must be measured by actual observations.

In 1862 Bunsen and Roscoe worked out a method of determining the intensity of light, by noting the time required for the darkening to a standard grey tint of paper impregnated with silver salts. Roscoe subsequently made a number of observations under different conditions and in different parts of the world by this method, and laid the foundation of what is known to meteorologists as "Photo-chemical Climate"; which is so-called because silver salts only measure the intensity of the *chemical* rays at the blue end of the spectrum. For a first treatment of the subject these rays may give a proportional measure of the total light.[1]

In 1877 Hartig, in a short note, was the first to suggest the desirability of actual photometric studies in relation to vegetation, especially of the light prevailing in the depths of forests. His idea was never practically developed.

In 1893 Wiesner worked out a convenient technique for thus measuring illumination, and proceeded to investigate the distribution of vegetation in association with it. An arbitrary unit of light-intensity was adopted, to wit, that light which darkens the photographic paper to the standard grey tone in one second. In the middle of the most brilliant summer days in Vienna the light-intensity may rise to 1·5 on this standard. The maximum intensity of total light (*i.e.*, direct sun *plus* diffuse light) varies from place to place with the height above the sea, *i.e.*, with the thinness of the absorbing atmosphere. In Europe at 384 metres elevation, maxima of 1·7 to 1·9 may occur, while on a few chance days at Yellowstone Park (3,000 metres elevation) maxima above 2·0 were observed with the sun at 52°. In Buitenzorg with mid-day sun at 87°, no value above 1·6 was recorded, but there the middle of the day was always somewhat clouded.

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[1] Professor Wiesner describes the preparation of a new sensitive paper—Rhodamin B. paper—which is acted on by all spectral rays, especially the yellow.

Besides the intensity of the light, its duration is obviously of biological importance. Here latitude makes an enormous difference, for during the vegetative period the sun is above the horizon for twenty-four hours in the arctic region, and only twelve in the tropics. Attempts are made to express this difference by computing daily "light-sums[1]." The highest actually observed in Vienna during 1894 was 419 on June 17th, and the lowest 6·2 on November 17th. It is not generally realised how much less the average daily light-sum is in winter than in summer. In January the average amount is 15·1 and in July 274·5. This means that if a plant could assimilate CO_2 all day, and in proportion to the intensity of the illumination, it might accumulate nearly twenty times as much organic matter in a mid-summer day as in a mid-winter day.

At Buitenzorg, although the sun rises higher in the heavens, the actual observed light-sums were smaller than those of summer in Vienna, presumably due to the shorter day and more absorbing atmosphere. Thus Wiesner for the former place computed 252 in November and 227 in January.

In Spitzbergen, in August, where the sun only rises to about 27° above the horizon, the light-sum observed was 97, while at Vienna, on such winter days when the sun also only rises to 27°, the shorter day reduces the light-sum to 35—50.

II.

From this sketch of photo-chemical climate and the amount of light incident upon vegetation we may now turn to the individual plant and its illumination.

The eye cannot be trusted to estimate the illumination of individual plants. A herb growing near a wall looks fully illuminated, but of course the wall must exclude nearly half the light of the sky, and measurement by exposing sensitive paper, shows that the intensity of illumination is about half that prevailing with a plant in the open. At the foot of a leafless tree in winter, even on the sunny side with the sun shining, there is a marked falling off in total illumination due to obstruction of much of the diffuse sky-light by the tree. On a sunny day in March, when the total light in the open was

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[1] Comparisons of light-sums may be made by plotting the daily curve of intensity with hours as abscissæ, and estimating the area enclosed between the curve and the base line.

0·427, near the tree on the sunny side it fell to 0·299; (on the shady side it was only 0·023).

Few plants are exposed to the full value of illumination, as they would be in a large plain with their leaves horizontal and all unshaded by one another, or by adjacent plants. In herbs the self-shading of parts is small, but in trees it is very large and there results a hollow centre to the tree where light is insufficient, surrounded by a shell of illuminated leaves. Some trees have open crowns like Pinus, into which the light can penetrate, others have closed crowns. Cypress is an extreme case, where the green shell, 20 cms. thick, surrounds a hollow space (about 72% of the whole volume) in which all leaves are dead.

In Nature any given species tends to have only a *restricted* range of natural illumination and Wiesner started out to record these relations and as far as possible to give a physiological explanation of them. He introduced the term Lichtgenuss (literally, light-use or light-enjoyment; "photic ration" of some translators) to express the degree of illumination in which a plant is found in Nature.

We may now proceed to define precisely the different light-relations to which quantitative values have to be given in this connection.

There is first the degree of illumination prevailing on any more or less shaded individual plant. This may be expressed, relatively to the total light on a freely exposed spot, by a fraction, say $\frac{1}{7}$. Such a fraction would mean that if simultaneous exposures of sensitive paper were made in the two places, the paper in the shaded habitat would take seven times as long to reach the standard tint as the paper in the fully exposed spot. Such a comparison can be made at any time of day and might be called the *individual* Lichtgenuss of the plant. When a number of different individuals of a species in the same locality are measured up in this way the fractional illumination will not be precisely the same for all: there will be a maximal and a minimal Lichtgenuss. The range of the fractions (writing the numerator as 1) expresses the Lichtgenuss of the species which I propose to term the relative Light-range (Rel. L.R.). Thus *Poa annua*, Rel. L.R.$=\frac{1}{1}$—$\frac{1}{8}$ means that individuals of this species were found in fully exposed spots and also in shaded spots where the light did not however fall below $\frac{1}{8}$ of the full light in the open.

In different latitudes and at different altitudes a given species does not exhibit the same Rel. L.R. Larger fractions of the light seem to be required in places, like the extreme north, where the general intensity of the light is less. It therefore becomes interesting to know in *absolute* measure the Lichtgenuss of plants. The absolute Lightgenuss of an individual plant corresponds to the intensity, in Bunsen-Roscoe units, of the light falling on it at the brightest time of an average day during its active vegetative period.

In practice an approximation to this is made by multiplying the Lichtgenuss fraction into the average mid-day light-intensity for that locality and that season of the year. In a region when this equalled 0·893 units, the Rel. L.R. given above for *Poa annua* would correspond to Abs. L.R.=0·893—0·297.

Wiesner has in this way expressed the distribution of *Poa annua* at different times in early summer. This grass appears in more and more shaded spots as the year wears on. Thus near Vienna he found :—

Early March, Rel. L.R., 1—$\frac{1}{3}$ and Abs. L.R., 0·89—0·29.
Early April, „ 1—$\frac{1}{4}$ and „ „ 1·00—0·25.
End of April, „ 1—$\frac{1}{7}$ and „ „ 1·10—0·15.
Middle of May „ 1—$\frac{1}{14}$ and „ „ 1·30—0·09.

At Cairo, early in March, the Rel. L.R. of this grass is 1—$\frac{1}{11}$, but in March the sun at Cairo is as high as it is in Vienna at the middle of April when Rel. L.R.=$\frac{1}{1}$—$\frac{1}{7}$. These higher minima in Vienna are attributed to the colder temperature prevailing at the corresponding time of year.

Poa annua does not tolerate deep shade, but exhibits a high light-range. This is true of grasses in general, though, some shade-grasses extend into the shade of European woods where the light is only $\frac{1}{50}$ or 0·02 ; and into tropical woods to $\frac{1}{100}$=0·015. In the deepest shade in woods they are, however, absent.

In considering the L.R. of trees we have the complication that the inner foliage of the crown is shaded by the outer. For ordinary trees the outer foliage is exposed to the full light of day. The illumination of the innermost leaves is measured by following down a branch into the crown until the innermost leaf is arrived at and here the sensitive paper is exposed. If the time taken to attain the standard grey is fifty-five times as long as when the paper is exposed on the free surface of the tree, then the Rel. L.R. of the tree is $\frac{1}{1}$—$\frac{1}{55}$. The implication is that the tree could just live in such a light as sustains its most shaded leaves.

Before all the leaves of the year are fully developed, higher minimum values are found, but in summer the minimum soon becomes stationary.

The minimum values observed for the light within the crowns of different trees near Vienna are very different (being of course a direct measure of the density of the foliage).

Buxus $\frac{1}{108}$ or 0·012. Populus alba $\frac{1}{12}$ or 0·085.
Fagus $\frac{1}{85}$ or 0·015. Larix $\frac{1}{5}$ or 0·250.

Dimly lighted as are the interior leaves of umbrageous trees yet plants are found to grow in the shade beneath them. In a pine wood the prevailing light on the ground may fall to $\frac{1}{80}$ or $\frac{1}{90}$. Under the trees in $\frac{1}{60}$ *Vaccinium myrtillus* may yet be found, in $\frac{1}{80}$ *Pteris aquilina* and in $\frac{1}{70}$ *Oxalis acetosella*: in less light than this nothing occurs, and a "dead" shade results. In tropics the "dead" shade comes at about $\frac{1}{120}$ which represents nearly the same absolute light-intensity as $\frac{1}{90}$ in Europe.

For all shade-bearing Phanerogams *Aspidistra elatior* seems to hold the record, for it struggles on in the darker parts of many a dwelling room where the light is about $\frac{1}{300}$ of total outside daylight.

Detailed data of the Lichtgenuss of a number of plants are to be found in Wiesner's book: an interesting systematic study of a district by these photometric methods forms a part of Hesselmann's paper on "Schwedischer Laubwiesen"; see Botan. Centrlbl. Beihefte, Bd. XVII., 1904.

III.

We now have to face the fundamental question—What is the physiological significance of the different ranges of illumination in which plants exist?

This is not at present definitely answerable. To a preliminary physiological analysis of Lichtgenuss Wiesner devotes a chapter of his book, and he concludes that the limits of the light-range of a plant are determined by the interaction of numerous physiological factors of which assimilation of CO_2 takes a place in the first line. This is held to be broadly due to effective assimilation ceasing at the lower limit of the light-range; a view inadequately based on the observation that at mid-day in summer an Acer or Fagus shows abundant starch in its outer leaves and diminishing quantities in the inner leaves till the innermost show little or none.

Secondarily the natural light-range is held to be determined by the well known fact that plants grown in light below the natural minimum do not attain the normal form, but show more or less of etiolation. Now, one of the characteristics of etiolation is a less resistance to external conditions—rain, fungi, etc., and it is interesting to note that in Nature one does not find, generally, in sub-minimal light, etiolated specimens but simply no specimens at all. This is interpreted as the result of the struggle for existence with more acclimatized competitors. Wiesner holds, from his experiments on growing Hepatica in different illuminations, that reduced leaf-structures occur in *excessive* as well as in subminimal light. He therefore regards the natural light-range as corresponding to an "*optimal* light-need."

It must be pointed out in criticism that the terms optimum and maximum are used by Wiesner in a quite uncritical way. There is no evidence for most plants that the full open light of nature is a *maximum* for them in the physiological sense of a cardinal point. It may be the maximum light occurring naturally, just as 0·03% is the maximum amount of CO_2 occurring naturally, but neither is a maximum in Sachs' sense. Also, for plants which seem to flourish best in full open light, the optimum illumination is said to be identical with the cardinal maximum, a very unsatifactory conception.

Critical experiments have never yet been made to try whether a plant which normally grows fully exposed to sun *plus* diffuse light utilises in *any* way *all* the light that falls upon it.

It is clear that it cannot use the full intensity for assimilation, as the supply of CO_2 is not adequate, but possibly the full intensity might not be wasted in forwarding some important but minute metabolic changes. Then again the form of the plant is to a certain extent a response to the stimulus of light, and the full sum of light might be significant in determining small points of form that have biological importance.

Experiments have been made to compare cultures grown in full and diminished illumination, but no one has yet proposed to cut out direct sunshine, while retaining *all* the diffuse light of the sky.

If a plant is grown on the north side of a wall so high that no sun reaches it in summer, then this wall will necessarily stop out, and that continually, the diffuse light from all parts of the sky that the sun traverses. This involves a reduction of the diffuse light by at least a third.

Before explaining how direct insolation could be extinguished without decreasing seriously the diffuse light we may consider such experiments in this direction as are at present recorded.

Wiesner experimented on small Beech trees in pots placed in four different lights, from April 9th to the middle of June. One of the trees was placed in the full open light and three others to the North, East and South of walls of such height that each received about a quarter of the sum of the full *diffuse* light which fell upon the plant in the open. As regards the *sunlight* none ever reached the north plant (N), while the east plant (E) got the morning sun, the south plant (S) the mid-day sun, and the plant in the open (O) the whole of the sun.

The first leaf-tip appeared:—N., April 20; E., April 16th; S., April 13th; O., April 13th. The development of the leaves occupied N., thirty days; E., twenty-two days; S., twenty-two days; O., twenty-two days. The same numbers of leaves were formed in all the positions, but the total fresh weights of leaf were different, being N., 52; E., 60; S., 74; O., 100.

The conclusion reached is that diffuse light alone suffices for normal leaf-development of the Beech, but that direct insolation hastens and promotes this development.

Recently Strakosch[1] has carried out experiments on the influence of sun and a diffuse light on that characteristic sun-plant the Sugar-beet.

The shaded plants were under a framework of planks and fine gauze, exposed to a light estimated at three-quarters of the total diffuse light, and no direct sun. When compared in October with the control plants grown in full sunshine, it was found that the shaded leaves were 10% smaller and 25% fewer. The difference in the roots was very marked, the average weight being 58 gr. in diffuse light and 190 gr. in sun, both containing about 12% of sugar in their juice.

Here again the plants come to normal development in diffuse light, but are larger in the sun. The marked preponderance of the insolated root suggests a direct result of higher temperature of the soil in the sun. Of course, one of the main points for critical work is to distinguish between the effect of the light of the sun as such and the vigorous heat-radiation which naturally accompanies it. Such separation could be accomplished by passing the radiation through a thin layer of water, but experiments on a big scale have yet to be carried out in this way.

A complete exclusion of sunlight without serious diminution of diffuse light could be carried out by means of a sort of "negative heliostat," a clockwork arrangement which would always cast a just sufficiently large shadow on the spot where the plant was placed, while yet the shadow-producing plate was sufficiently remote not to interfere with the diffuse light from the sky. This might be done by having a very long pole fastened to the earth at one end by a pivot so that it could be rotated in any plane diurnally, and also be tilted each day so that its rotation might be in the same plane as that of the sun's apparent motion.

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[1] Oster-ungar. Zeitschr. für Zuckerindustrie, 1906.

If a shadow-board were fixed at right angles, at the free end of the pole, then it would always cast a shadow along the direction of the pole, and plants in pots ranged along its axis would be perpetually shaded from sunshine, but exposed to practically full diffuse light if placed near the centre of rotation and far from the shadow-board.

Plants grown under these conditions could be compared with fully insolated plants as regards fresh and dry weight and general development.

Then the question would have to be attacked as to how far sunlight can be replaced by dark heat-radiation. There are several facts which point to the importance of the heating effect of radiation. In arctic regions shade-plants hardly exist, and in all cases where a species has a wide distribution from North to South it is found that it has a bigger minimum of Rel. L.R. in its Northern habitats. Often, indeed, Wiesner remarks that sunlight, added to good diffuse light, hastens rather than modifies the development and further adds that broadly speaking it is on diffuse light that plants depend for their illumination, and that the illuminative value of the sun works rather through increasing this than by direct insolation.

Regarding Lichtgenuss with a quite open and sceptical mind, it does not then seem quite certain that the position of the plant in the observed range of lights is really directly determined by the light itself. In most climates both temperature and transpiration march parallel with illumination, and either of these might have an important influence in determining the exact range of comfortable existence for a given plant.

Further, light when it is the *vera causa* need not exhibit a uniform relation between its intensity and the magnitude of the effect.

Thus in assimilation of CO_2 a limit is set by the CO_2 naturally available, and when that amount is attained, further increase of light should not cause increase of assimilation. All available exact evidence is against the upper ranges of illumination being sought by plants for the purpose of increased assimilation. The duration of illumination might well on the other hand be in direct relation to the accumulating amount of assimilated products; but these considerations, worked out in the laboratory, have yet to be transferred to purely natural conditions. It may well be that the lower limit of light-range is determined by assimilation and the upper by some quite different cause.

The significance of Lichtgenuss still awaits fundamental investigation, but to Wiesner we are indebted for a very precise and full knowledge of the relations that hold in Nature.

F. F. B.

THE ORIGIN OF TRIPLE FUSION

A SUGGESTION.

By EMILY M. BERRIDGE, B.Sc.

[TEXT-FIG. 17].

THE problem of the origin of the Angiospermic endosperm, which, after the discovery of double fertilization and of the unique process of triple fusion, seemed to become more intricate and more difficult of solution than ever before, has recently been attracting a considerable amount of attention.

Within the last year two papers have appeared dealing with the question, both authors basing their views mainly on recent work carried out by American botanists on the embryogeny of the Gymnosperms, while a third suggestion has been brought forward by Dr. Land in his paper on *Ephedra trifurca.*

Dr. Land (1) describes a peculiar process of tissue-formation within the upper part of the archegonium of this plant, which he regards as the precursor to endosperm development among the Angiosperms. This curious tissue also occurs in *Ephedra distachya* about the time of the commencement of pro-embryo formation, and arises in exactly the same way; first a fibrillar structure appears in the cytoplasm, linking together the free fragments of chromatin material introdued by the proteid vacuoles, and then each fragment surrounds itself with a tiny zone of cytoplasm and a delicate cell wall. Dr. Land regards this tissue-formation as the result of the disintegration of a certain nucleus lying near the apex of the archegonium, which he considers to be the second male nucleus, but which from its position and size, appears extremely like the persistent ventral canal-nucleus frequently found in other species of *Ephedra*. For the first or functional male-nucleus is distinctly smaller than the ventral canal-nucleus, and the second male-nucleus is certainly not larger than the first. The latter was identified in the slides made by Miss Sanday for a previous paper in this Journal (2) in five separate cases, once close to the egg-nucleus, twice well on its way toward the latter, and twice near the tip of the pollen-tube; it is only 8 to 13μ in mean diameter, while that of the ventral canal-nucleus varies from 19 to 30μ. The size of the male-nuclei is therefore comparable with that of the generative nuclei in Angiosperms; in this respect the Gnetaceæ may show a Pro-angiospermic character. The fact certainly accounts for the difficulty, experienced by all investigators, in identifying with any certainty cases of actual fusion of the gametes in this group.

But whether this evanescent "physiological endosperm" described by Dr. Land be produced by the interaction of the chromatin of disintegrated jacket-nuclei with that of the second male nucleus or is merely a complicated example of nuclear disintegration such as was observed by Murrill in *Tsuga canadensis*, a view suggested by its occurrence in cells other than the archegonium, it is distinctively a degenerative tissue, and hardly likely in the course of evolution to replace, as a nutritive tissue, the jacket and prothallial cells which at this time are showing signs of renewed activity and vigour.

It must be admitted, however, that it is closely associated with a process of pro-embryo formation from which, as I hope to show, the endosperm of the Angiosperms may have originated.

An objection on somewhat similar grounds may be urged against the theory lately brought forward by Dr. Otto Porsch (3), in a lengthy communication consisting to a great extent of a summary of recent work on the Gymnosperms, together with a few original observations on *Ephedra distachya*. He regards the embryo-sac as homologous with two fused archegonia each consisting of a tetrad of nuclei, *i.e.*, two neck-cells, an egg-cell, and a ventral canal nucleus. Practically the same view was brought forward by Professor Hartog in 1891 (4), though expressed in somewhat more general terms. The synergidæ and the two lower antipodals are by this author regarded as neck-cells of reduced archegonia, and the four nuclei which lie more centrally in the sac, *i.e.*, egg-nucleus, polar nuclei and upper antipodal nucleus, as four gametes.

According to Dr. Porsch's view, the two polar nuclei are the equivalents of the two ventral canal nuclei. But of all the nuclei associated with or forming part of the archegonium in Gymnosperms, the ventral canal nucleus is the one which shows, as a rule, least vitality, and that there should exist a tendency for two precisely similar nuclei of low vitality to fuse together, seems most improbable. Also it seems unaccountable that the antipodal egg should have lost all affinity for the second sperm nucleus, while the antipodal ventral canal nucleus should have developed such an attraction, particularly in chalazogamic families, which Dr. Porsch regards as primitive.

The suggestion that the ventral canal nucleus may be the homologue of the upper polar nucleus, has been brought forward by Miss Thomas in a historical sketch of "double fertilization" in "Science Progress" (5). In this case it may be conjectured that the original lack of vitality is made good by fusion with a nucleus of differing nature, or that possibly the latter supplies some element necessary, in most cases at least, to make fertilization by the second male gamete effective. For it is evident that though both the ventral canal-nucleus and the upper polar-nucleus are sisters of the functional egg-nucleus, they are not equivalent to it.

This latter view then accounts for the relationship of the egg and upper polar nucleus, and a physiological reason for the occurrence of triple fusion is, perhaps, indicated by it. But direct evidence that the ventral canal nucleus ever fuses with another nucleus of any kind is wholly wanting, and the opinion that it is occasionally fertilized rests on rather a slight foundation, for even that based upon Dr. Land's observations of nuclear divisions in the apex of the archegonium of Thuja (6) is somewhat weakened by the fact that it was found to divide before as well as after fertilization.

As an alternative to this hypothesis, it may be pointed out that earlier in the history of the Gymnosperm ovule we have another series of sister-nuclei, which may equally well be homologized with those of the Angiosperm embryo-sac. In *Ephedra* there can be distiuguished, among the free nuclei found, prior to the formation of the prothallial tissue, a small group lying at the apex of the sac, which gives rise to the archegonial region, *i.e.*, that consisting of archegonia and jacket cells. These nuclei may be divided into two classes, those, which, after forming short alveoli, undergo but one division, so that the alveolus is divided into but two cells, the primary neck and central cells, and those which undergo a series of divisions, so that a row of jacket-cells is formed within it. These two sets of nuclei may be called respectively archegonium and jacket-cell initials; that they are very similar in character is evident from the strong likeness between the cells they give rise to, a likeness worked out in detail in a previous paper on *Ephedra distachya* (2), and much insisted upon by Dr. Porsch, who gives an excellent figure of egg-like jacket-cells.

There must, however, be some slight difference determining which of the nuclei shall be archegonium and which jacket-cell initials, and an important consequence of this difference is that the egg-nuclei descended from the one set are capable of direct fertilization by sperm-nuclei, while the jacket-nuclei derived from the other set, if not actually incapable of direct fertilization, certainly never become fully-matured gametes.

It is, nevertheless, a significant fact that in *E. distachya* certain of these latter nuclei, under the stimulus imparted to the whole archegonial region by the entry of the pollen-tubes, and probably in all cases after fusion with another nucleus, show signs of proceeding to the formation of embryos. Within the jacket-cells themselves, where the stimulus from the pollen-tube must be slight and indirect it usually goes no further than the development of a radiating zone of cytoplasm round certain of the nuclei, but when the latter have escaped into the archegonium, or are only separated from it by an extremely thin wall, there is outgrowth of these pro-embryonal cells into primary suspensors occasionally bearing rudimentary embryos at the tip. That this potentiality is present in the jacket is demonstrated not only by the behaviour of these cells in *E. distachya*, but is evidently clearly indicated in *E. trifurca*, though it does not appear to reach such a degree of effective development here as in the European species. Dr. Land repeatedly remarks on the likeness of the jacket-cells to eggs, and says that "Apogamy was at first suspected, but further study showed that these egg-like jacket-nuclei do not function, being finally broken down and absorbed by the pro-embryos." Drs. Cavara and Rogasi also mention the formation of pro-embryos by jacket-nuclei in *E. campylopoda*. The fusions preceding pro-embryo formation of this nature in *E. distachya* are not always confined to jacket-nuclei, in several cases it was observed that the nucleus of an ordinary prothallial cell had entered a jacket-cell adjacent to it. Also in one case, represented in Fig. 17, fusion between a jacket-nucleus, and a nucleus from the pollen-tube seems imminent. This, the first jacket-nucleus to escape into the egg-cell, is apparently attracted by the proximity of the contents of the pollen-tube[1]; the ventral canal-nucleus, though still quite recognizable, appears to be in a dying and inactive condition.

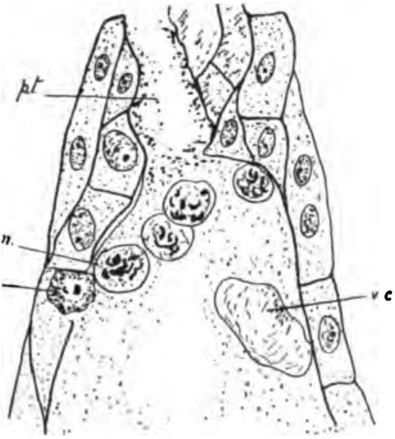

Fig. 17. Jacket-nucleus entering apex of archegonium containing four nuclei from the pollen-tube. *j.n.*, jacket-nucleus ; *p.t.*, pollen-tube ; *p.n.*, nuclei from the pollen-tube ; *v.c.*, ventral canal-nucleus.

Here therefore we have a process occurring in the embryo-sac of a Gymnospermic genus, which shows a remarkable likeness to the development of the Angiospermic endosperm after triple fusion, that is to say, we have cell-formation resulting from the fusion of nuclei, one of which at least is allied to the egg-nucleus, and taking place under the stimulus due to the entry of the pollen-tube.

Moreover, if the polar-nucleus is regarded as the homologue of the jacket-initial-nucleus, it is possible to trace among the eight nuclei of the Angiosperm embryo-sac representatives of the four classes of cells which we find in the sac of *Ephedra* and other Gymnosperms.

1. The egg-nucleus in Angiosperms is homologous with the initial nucleus of the archegonium which, as in *Gnetum*, matures without the formation of that organ; it therefore represents the latter.

2. The synergidæ probably represent the cells in the upper part of the prothallium, whose only function appears to be the

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[1] I have not been able to trace the origin of these pollen-tube nuclei, several of which in this case have the appearance of gametes, but there are indications, even when the tube is still within the pollen-chamber, that more than the four nuclei seen by Dr. Land in his artificial cultures are formed.

nutritive one common to the whole, but which, as Strasburger suggests, have assumed in Angiosperms a new one in relation to the pollen-tube.

3. The antipodal nuclei represent the nutritive and haustorial cells which compose the lower part of the prothallium.

4. The upper polar nucleus represents the jacket-cells, which, though not as a rule capable of fertilization, yet after union with another nucleus, appear to be in a condition to receive stimulus from the contents of the pollen-tube and to proceed to the formation of pro-embryos. Since in the Angiosperm embryo-sac there is reduction to one solitary nucleus, the stimulus from the pollen-tube naturally takes the form of fusion with the second male gamete.

This view of the organization of the Angiosperm embryo-sac is strongly supported by Dr. Lotsy's observations on *Gnetum Gnemon* (7), although it differs widely from his own interpretation, which is based to a considerable extent on the exceptional case of *Balanophora*.

Drs. Coulter and Chamberlain remark in their well known book on "The Morphology of the Spermatophytes," with reference to the embryo-sac of *Gnetum Gnemon*, "The strong polarity of the sac, the occurrence of naked eggs, the large or entire development of endosperm-tissue after fertilization, are all features suggestive of the Angiosperm condition. Especially striking in comparison with the Angiosperm embryo-sac is the occurrence of free cells at the micropylar end of the sac and of a compact tissue at the antipodal end." When we note that this post-fertilization endosperm is initiated by nuclei indistinguishable from and closely related to the functional eggs, and commences with the formation of cells resembling the zygotes or pro-embryos in everything except size, there seems very little doubt that these are homologous with the jacket-nuclei of *Ephedra*, though Dr. Lotsy does not mention the occurrence of any fusions among them. From an examination of the figures it also appears within the bounds of possibility that the functional paired zygotes may be daughter-nuclei of the fertilized egg, which has thus far retained the tendency to divide shown by almost all other Gymnosperm fusion nuclei, in which case the second sperm-nucleus might be involved in the production of these weaker pro-embryo-like cells which are here called retarded prothallium cells. It is quite conceivable that this nutritive tissue, lying in close contact with the newly formed pro-embryos, would ultimately replace the more distant prothallial tissue at the base of the sac.

An endosperm having an origin such as that outlined above, would be of pro-embryonal nature, but derived from cells which had already, earlier in their phylogenetic history, assumed a nutritive function. Thus two views very generally held with regard to the endosperm of Angiosperms, first that, being a nutritive tissue, it must be prothallial, second that, being a product of fertilization, it must be an embryo, would be hereby reconciled. Moreover the suggestion made by Miss Sargant (8) (to whom I owe much kind and suggestive help), that the endosperm is to a certain degree a monstrous embryo, owing to some want of balance in the constitution of its nuclei due to its threefold parentage, is in no way precluded.

Further careful investigation of the Gnetaceæ is needed to give this theory a sure foundation in fact; unfortunately the readiness with which these ovules fall a prey to insect attacks is a serious obstacle to their study. Only when the fate of the second male nucleus has been determined with certainty in forms which are more or less closely related to the ancestors of the Angiosperms, as these seem to be, will a final solution of the problem be possible.

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RECENT BOTANICAL APPOINTMENTS.

Mr. R. H. Lock has been appointed to a new post, the Assistant Directorship of the Royal Botanic Gardens, Peradeniya, Ceylon.

Dr. C. E. Moss, of Manchester, will succeed Mr. Lock in the Curatorship of the Cambridge University Herbarium.

Miss H. C. I. Fraser, D.Sc., has been appointed Lecturer on Botany at University College, Nottingham.

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